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Articles dealing with any phase of botany relating to the Upper Great Lakes Region may be sent to the editor in chief. In preparing manuscripts, authors are requested to follow our style and the suggestions in "Information for Authors" (Vol. 15, p. 238).

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PLANT COMMUNITIES OF THE SAND DUNES REGION OF BERRIEN COUNTY, MICHIGAN

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The shoreline of Michigan is some 3,540 km (2,200 mi) in length, and of this 450 km (280 mi) or 13% qualify as coastal sand dunes (Lewis, 1975). In 1976 more than 5,000,000 tons of sand were mined in Michigan, with a value in excess of \$40,000,000 (Ayres et al., 1978). Dune sand is highly desirable for industrial uses such as foundry castings, glass-making, and scouring agents because of its purity and rounded grain structure (Fig. 1). Public attention to coastal dunes was heightened when Governor Milliken on July 30, 1976 signed into law House Bill no. 4038. Under this statute, known as the Sand Dune Protection and Management Act (Act no. 222, P.S. 1976; M.C.L. 281.651-281.664), proposed sand mining activity is reviewed, and environmental effects are required to be evaluated and monitored before a permit is granted. Sand dune areas are legally designated as "geomorphic features composed primarily of sand, whether wind-blown or of other origin and which lie within two miles of the ordinary high water mark on a Great Lake." The Department of Natural Resources, under this law, is required to make several types of studies relating to Michigan's dunes, including certain vegetation analyses. This report results from the first two years of our continuing sand dunes vegetation analyses carried out under the provisions of Act no. 222 and supervised by the Department of Natural Resources.

One of the nation's most impressive dune systems borders the eastern shores of Lake Michigan. Buckler (1978) pointed out that these unique dunes collectively represent the world's largest accumulation of sand bordering a body of fresh water. Extending from Michigan's southwestern boundary to the Straits of Mackinac, they consist of a most diverse pattern of features. The shoreline is marked with broad sandy beaches, low shore foredunes, massive dune bluffs—some open and desert-like, others stabilized with a rich hardwood forest cover. These natural features are of vital importance to the state's economy because the superb scenic values of duneland serve as a magnet for the tourist industry, as do the opportunities for water sports, hiking, and camping. In some instances this rugged dune country is the last refuge for unique assemblages of plants and animals.

One of the most interesting sections of duneland is that located in Berrien County (Fig. 2) known as the Grand Mere area. It extends from the village of Lakeside northward to the vicinity of Glenlord Road at the southern edge of St. Joseph. It is hemmed in on the east by the postglacial feature known as the Covert Ridge. In this region the Red Arrow Highway (US-12) follows the top of this ridge. This report, however, will deal only with that section of Berrien Co. north of Warren Dunes State Park. It is characterized by a great diversity of topography and other natural features which include open dunes,

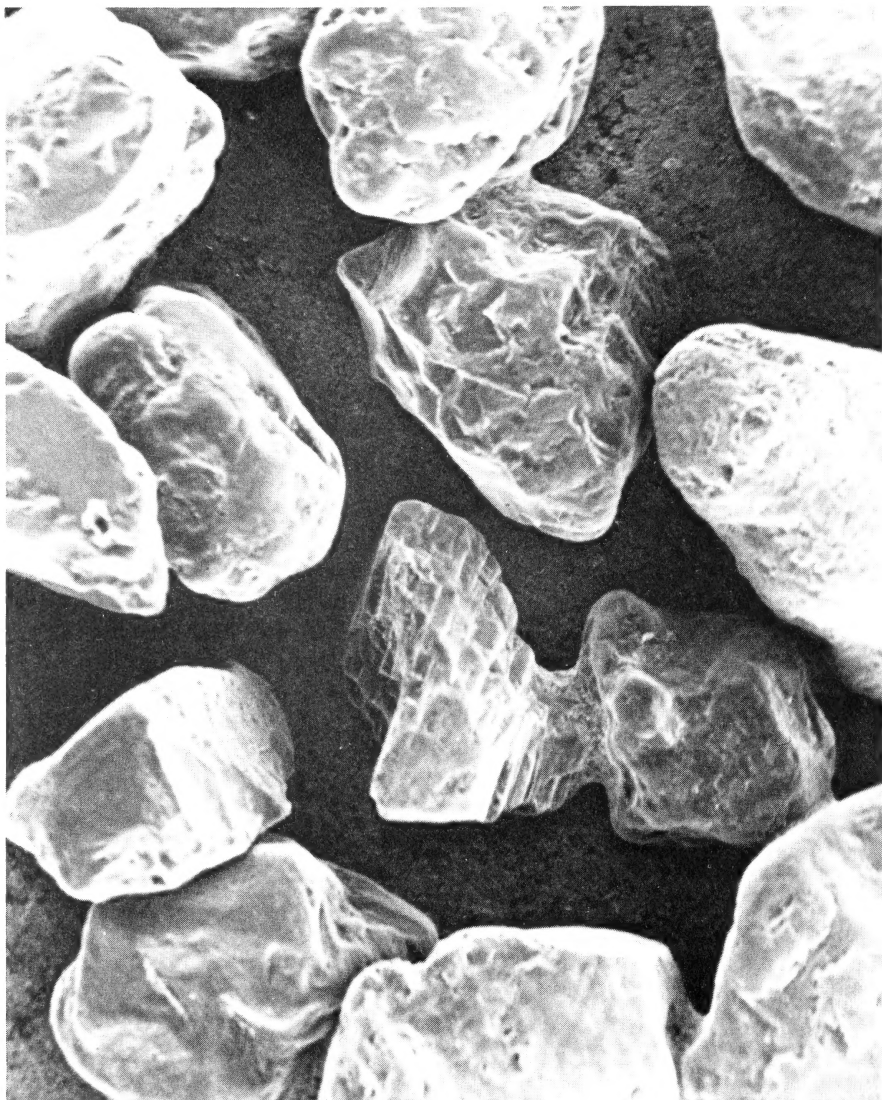


Fig. 1. Scanning electron micrograph of Lake Michigan beach sand from Berrien Co., (X112). Courtesy of Peter B. Kaufman and Myong Lee, University of Michigan.

oak woods, beech-maple forests, hemlock stands, shoreline strips, swamp forests, and prairie, fen, and aquatic communities. The northern and southern sections, separated by Willow Road, contrast sharply with one another: The southern section is dominated by an extensive system of very rugged, high dunes and ridges,

whereas the northern, characterized by low wetland areas, consists of a huge post-glacial embayment area in which are located three interesting lakes.

The vegetation and ecology of Lake Michigan's sand dunes were of interest even before the turn of the century (Hill, 1893; Cowles, 1899). It was with the 1899 work of Cowles on sand dunes that basic principles of plant succession were developed in the United States. Further work on dune ecology helped pioneer our understanding of plant community relationships, resulting in the concept of "climax" vegetation which is defined in reference to a community that exists in a state of dynamic equilibrium with the environmental regime at that particular locality. A climax community would not be expected to undergo significant change in floristic composition and community structure with passage of time.

GEOLOGY

Michigan's oldest dunes, those of the Algonquin series, are about 13,000 years in age (Dorr & Eschman, 1970). Most of the coastal Lake Michigan dunes are of Nipissing age, about 3,500 years old, and as such are among the state's youngest geomorphic features (Buckler, 1978). These dunes were formed when the lake level was some 25 ft higher than present levels (Buckler, 1978), although many dunes continue to be rearranged due to the action of wind and water.

The formation of dunes along the Lake Michigan shoreline was made possible by conditions associated with Wisconsin glaciation. As the gigantic ice mass plowed down through the Lake Michigan and Lake Huron basins and reached its southern limits, vast quantities of glacial debris were piled into huge

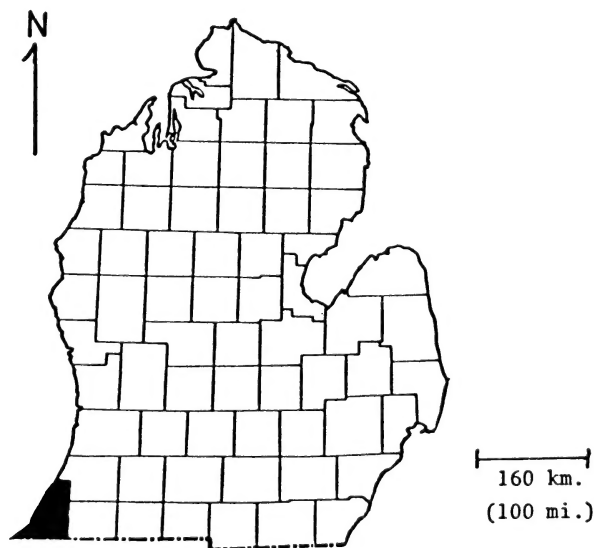


Fig. 2. Location of Berrien Co.

ridges known as moraines. Then as the ice melted and the glacier receded, the melt water trapped between the moraines and the retreating ice formed Lake Chicago. Several readvances of ice formed additional moraines and glacial lakes. Finally, the ice retreated north of the Straits, and the water in the Lake Michigan and Lake Huron basins combined to form Lake Algonquin at a level of 605 ft. This level, 25 ft higher than at present, was due to ice blockage of the normal outlet through the St. Lawrence River valley.

As the ice retreated farther north, the St. Lawrence valley was freed of ice. The St. Lawrence River valley was still depressed by the weight of previous ice loads, and a low drainage channel was opened toward the northeast. This depression of the drainage channel made possible greater flow from the Lake Michigan and Lake Huron basins some 9,500 years ago and resulted in the formation of Lake Chippewa at 230 ft elevation in the Lake Michigan basin and Lake Stanley at 190 ft in the Lake Huron basin.

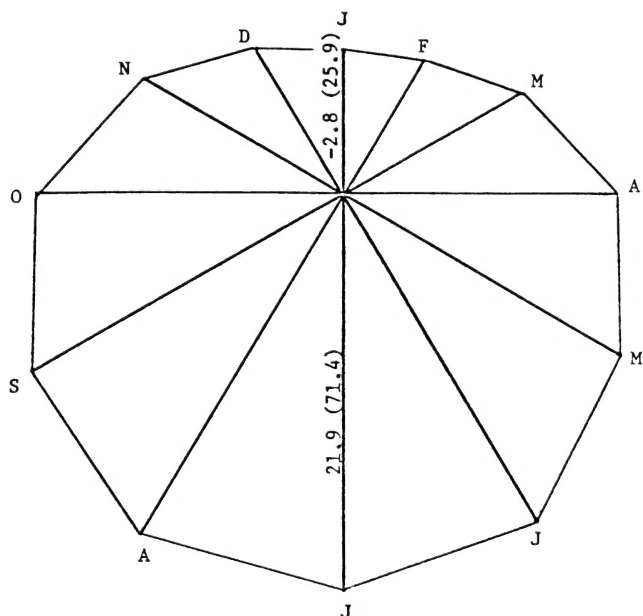
Eventually, the land along the St. Lawrence River valley, relieved of the weight of ice, gradually rebounded toward its originally higher level. About 4,000 years ago this resulted in a single glacial lake known as Lake Nipissing which occupied the Lakes Michigan and Huron basins at an elevation of 605 ft. Later, the St. Clair and Detroit River channels were eroded until the water level decreased to 595 ft and formed the Lake Algoma stage about 3,000 years ago.

With water levels at 605 ft elevation for both the Algonquin and Nipissing stages, considerable wave action eroded glacial debris along the shoreline. The waves separated gravel, clay, and sand components with the lighter sand grains being washed onto the beaches. (Wave action has the effect of rounding sand grains, Fig. 1, rendering them more desirable for certain industrial applications than the relatively more angular sand particles not so modified by wave action. Further rounding and smoothing is caused by collisions in blowing sand as it moves inland.)

Substantial dune formations require a large supply of sand together with relatively strong persistent winds to move it. These conditions prevailed during the two periods of maximum dune formation. Temperature differences between water and adjoining land masses often provided conditions which resulted in landward wind currents, and the large, open space over the lake surface gave further opportunity for wind velocities to develop. Consequently, tremendous dunes and dune complexes formed during the Algonquin and, especially, the Nipissing post-glacial stages. As a result, vast, open, desert-like dune complexes were formed at Sleeping Bear, Warren Dunes, Ludington, and Grand Marais. At other locations forest-covered dunes were modified by wind action opening up sandy channels called "blowouts" which today may be seen at Hoffmaster State Park and Cathead Bay and also in the Grand Mere area. Along other sections of the shoreline strong wave action cut into the bank leaving steep, open bluffs, while in still other areas "perched" dunes were formed on top of glacial moraines.

CLIMATE

Details of climate (Figs. 3–5) for the study sites are based on data from the closest weather stations at Benton Harbor (Berrien Co.) and Muskegon



Jan.	-2.8	(25.9)	July	21.9	(71.4)
Feb.	-2.4	(27.7)	Aug.	21.9	(70.1)
March	2.0	(35.6)	Sept.	17.8	(64.0)
April	8.7	(47.7)	Oct.	12.2	(53.9)
May	14.1	(57.3)	Nov.	4.9	(40.9)
June	19.8	(67.7)	Dec.	-1.1	(30.0)
Annual mean 9.7 (49.4)					

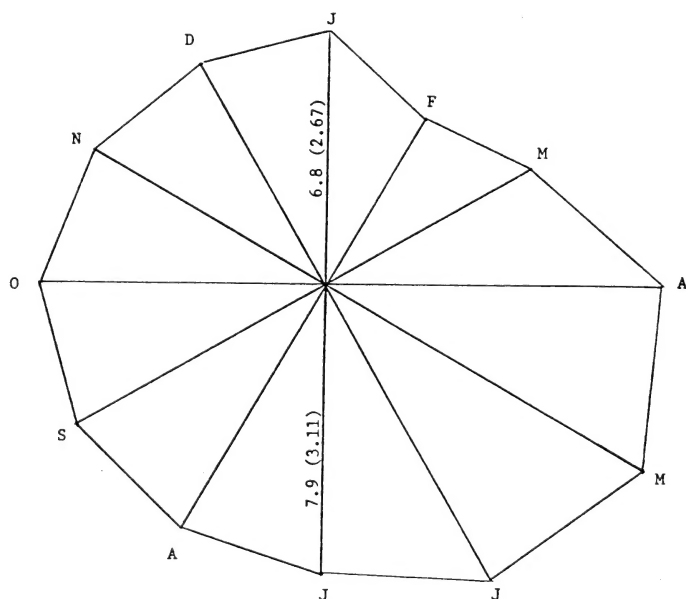
Fig. 3. Mean monthly temperatures, °C(°F), for Benton Harbor, Mich., for 1940-69. (Data compiled by U. S. Dept. Commerce, Nat. Oceanic & Atmos. Admin., and Mich. Weather Service.)

(Muskegon Co.), which lies four counties northward.

Mean monthly temperatures are listed in Fig. 3. The annual mean is 9.7°C (49.4°F) with the warmest in July at 21.9°C (71.4°F) and the coldest in January at -2.8°C (25.9°F). The moderating effect of Lake Michigan water temperature undoubtedly reduces the fluctuations to be expected farther inland. Westerly winds cause spring and early summer temperatures to be cooler than those farther inland. Likewise, the falls and winters are somewhat milder. This temperature regime considerably benefits agricultural pursuits. In the Benton Harbor vicinity the average date of the last freezing temperature is April 25, and the average date of the first freezing temperature is October 29. The freeze-free period averages 187 days (U.S. Dept. Comm., NOAA, 1971).

Mean monthly precipitation is depicted in Fig. 4. The annual mean is 90.7 cm (35.69 in), and precipitation is well distributed throughout the year. The least amounts come during February and March. Otherwise, the relative symmetry of the dodecagon (Fig. 3) graphically depicts even distribution patterns. Approximately 55% of the precipitation comes during the crop season—May to October. Snowfall averages 146.8 cm (57.8 in) annually. The first average one-inch snow depth is achieved by November 27, the first three-inch by December 15, and the first six-inch by January 5. (U.S. Dept. Comm., NOAA, 1971).

Mean prevailing wind directions are shown in Fig. 5; the broad line in the figure indicates the mean annual direction and speed which in this locality, Muskegon, is from a south-southwest direction at 17.5 km/hr (10.9 mph). Since most of the wind comes from this direction, one would expect to find the dunes



Jan.	6.8	(2.67)	July	7.9	(3.11)
Feb.	5.1	(2.02)	Aug.	7.6	(2.99)
March	6.3	(2.47)	Sept.	7.5	(2.97)
April	8.9	(3.49)	Oct.	7.7	(3.04)
May	9.7	(3.83)	Nov.	7.2	(2.83)
June	9.0	(3.55)	Dec.	6.9	(2.72)

Annual mean 90.7 (35.69)

Fig. 4. Mean monthly precipitation, cm (in.), for Benton Harbor, Mich., for 1940-69. (Data compiled by U. S. Dept. Commerce, Nat. Oceanic & Atmos. Admin., and Mich. Weather Service.)

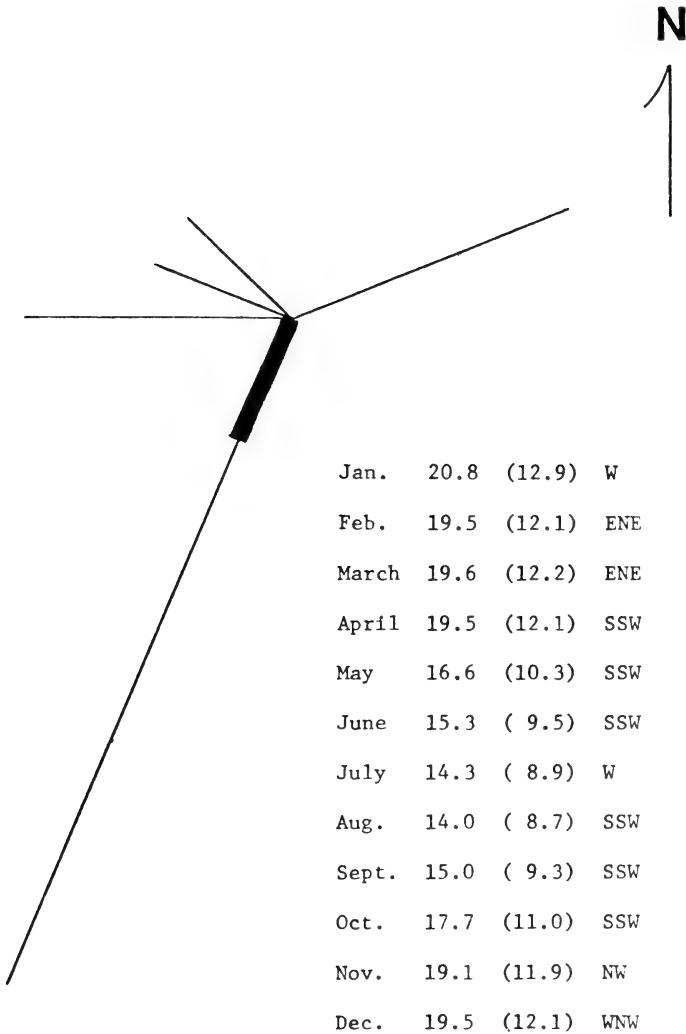


Fig. 5. Wind rose for Muskegon, Mich., showing mean wind direction and velocity km/hr (mph). Broad line indicates mean annual direction, SSW at 17.5 (10.9). (Nat. Oceanic & Atmos. Admin. Length of record: mean wind speed, 1959–77; prevailing direction, 1959–63.)

and their blowouts with a similar orientation. This is indeed the case as shown on the map (Fig. 6).

METHODS AND PROCEDURES

Our purpose in selecting different types of habitats for quadrat analysis was not only to show variation in floristic diversity but to gain some impression

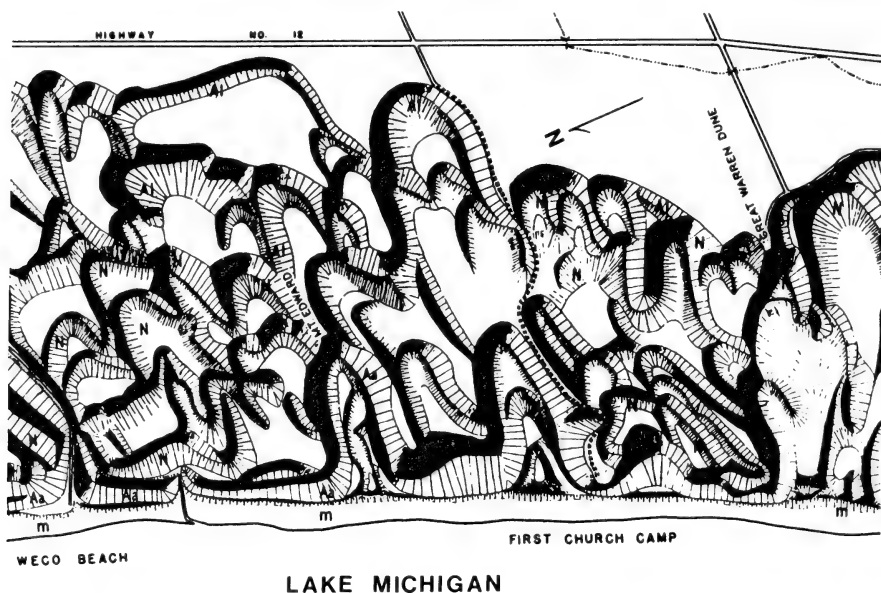


Fig. 6. Orientation of principal sand dunes in the Bridgman area (after Tague, 1947). Aa = Algoma, Al = Algonquin, N = Nipissing, m = present dune.

of the potential of the area both in terms of forest composition and relative abundance of species. Care was taken to adopt field methods which would be most useful and which would be employed for future site investigations. For estimating ground cover and understory density we used a scale adapted from Braun-Blanquet (1932) and Benninghoff (1966). This method was utilized by Sylvia Taylor of the Michigan Department of State Highway and Transportation in the Environmental Assessment for Reconstruction of US-2 in Mackinac Co. Study quadrats, measuring 20 m on a side, were oriented by compass along north-south and east-west lines.

The cover-abundance scale for species of ground cover was as follows:

- 5 = cover more than 3/4 of the area ($> 75\%$)
- 4 = cover 1/2 to 3/4 of area (50–75%)
- 3 = cover 1/4 to 1/2 of area (25–50%)
- 2 = cover 1/20 to 1/4 of area (5–25%)
- 1 = numerous but less than 1/20 ($< 5\%$)
- r = solitary with small cover

Estimation of understory composition was based on a tally of the total number of stems for each species, grouped as follows:

- 4 = over 100 individuals
- 3 = 11–100 individuals
- 2 = 2–10 individuals
- 1 = one stem only
- = stem off plot, overhanging into area

All tree species with stems at least 8 cm (3 in) diameter at breast height (1.3 m or 4½ ft) were identified and their diameters recorded separately. For these measurements a steel diameter tape was used. From DBH measurements basal area values were obtained and used as a measure of relative dominance of a given species within a quadrat. Analyses of basal area values by species and quadrat appear in Table 1.

Trips were made to the study sites during the growing seasons of 1979 and 1980. Voucher collections of vascular plants are on deposit at Cranbrook Institute of Science's Billington Herbarium. Identifications follow Gleason (1952) and Voss (1972).

POTENTIAL DUNE COMMUNITIES

The development of a Michigan dune requires that certain physical and biological parameters be working in concert. Sand and wind must be available in a climate where moderate growing conditions prevail. The dune initiating plants include trees such as cottonwood (*Populus deltoides*) and willow (*Salix* spp.), shrubs such as sand cherry (*Prunus pumila*), and several species of grass—particularly marram grass (*Ammophila breviligulata*). Such plants possess a unique ability for upward growth through the accumulating sand. Their differential ability for upward growth determines, to a certain extent, the height of dunes. Those dunes formed in association with marram grass are higher than those with grasses less capable of upward growth, and cottonwood trees form the highest dunes of all (Olson, 1958a).

From open sand to a dune covered by climax forest type a number of successional stages occur, each characterized by its own woody and herbaceous species. A simplified concept of these stages of plant succession appears below:

bare sand → beach grasses → deciduous shrubs → evergreen shrubs →
pine → black oak → beech-maple

The flora of Michigan sand dunes includes species with widely varying ecological amplitudes. Since these species did not likely evolve in the same place, it should not be surprising to see them growing elsewhere in habitats quite unlike those produced through the accumulations of large piles of sand. However, when one takes into account initial colonizing factors such as topography, climate, and physiography, a wide variety of dune community vegetation types emerge. A diagram relating these factors appears in Fig. 7.

DESCRIPTION OF PLANT COMMUNITIES

Our studies show a number of kinds of plant communities in the dune-lands of Berrien Co., including beach, dry forest types such as black oak, both hardwood and coniferous mesic forest stands, and wet habitats. Since both open water of small lakes and damp depressions were noted in the study site, we would anticipate the succession (depicted in Fig. 7) toward tall grass prairie or red maple swamp, both of which already occur in the region.

We believe that the sand has abundant water-holding capacity on certain high ridges. This opinion is based on the occurrence of such plants as leather-

Table 1. Tree basal area results from 20 m X 20 m plots.

Plot Slope				Number of trees, basal area (cm ²) and (% coverage)																				
No. of species	Total no. of trees	Total basal area (cm ²)		American elm	basswood	beech	bitternut hickory	black ash	black cherry	black oak	blue beech	chestnut oak	flowering dogwood	hemlock	hop hornbeam	papaw	red maple	red oak	sassafras	sugar maple	tulip-tree	white ash	white oak	yellow birch
1	flat	11	46	14,617	1 97 (0.7)	15 6,415 (43.9)		1 260 (1.8)			10 649 (4.4)		1 61 (0.4)				1 100 (0.7)			9 1,671 (11.4)	3 3,868 (26.5)	2 1,358 (9.3)		
2	flat	6	29	10,136		7 1,188 (11.7)				7 2,283 (22.5)					1 51 (0.5)		4 3,154 (31.1)		7 1,406 (13.9)				2 2,054 (20.3)	
3	27°E	2	26	11,779						23 11,005 (93.4)													3 774 (6.6)	
4	flat	3	14	12,503		6 3,335 (27.8)	5 6,746 (54.0)							3 2,422 (19.4)										
5	flat	9	19	17,957		7 5,258 (29.3)				1 65 (0.4)	1 543 (3.0)			1 64 (0.4)					2 1,376 (7.7)	2 1,094 (6.1)	3 3,257 (18.1)	1 1,058 (5.9)		1 5,242 (29.2)
6	12°E	4	17	21,187			2 4,025 (19.0)		1 1,598 (7.5)					13 14,518 (68.5)							1 1,046 (4.9)			
7	flat	7	16	12,596		4 1,916 (15.2)		1 177 (1.4)				1 281 (2.2)							6 5,789 (46.0)	1 495 (3.9)	3 3,983 (31.6)			
8	30°N	4	12	12,872		4 8,335 (64.8)	1 201 (1.6)							4 3,123 (24.3)							1 1,213 (9.4)			
9	30°E	7	23	15,926		4 2,050 (12.8)	2 332 (2.1)		3 2,198 (13.8)				1 87 (0.5)						8 8,880 (55.8)	4 1,639 (10.3)		1 740 (4.6)		

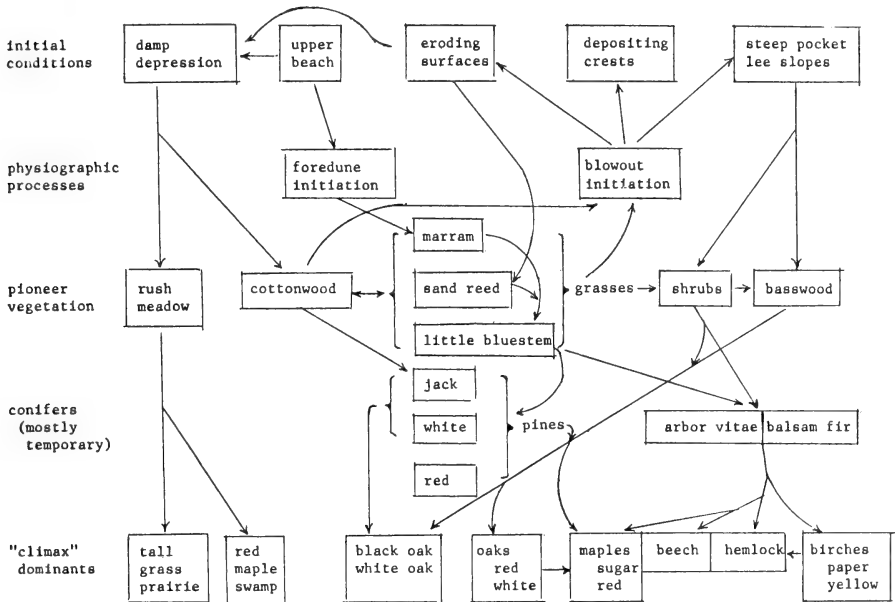


Fig. 7. Successional relations of dune vegetation (modified from Olson, 1958b).

wood (*Dirca palustris*), red osier (*Cornus stolonifera*) and blue beech (*Carpinus caroliniana*), species which typically occur in low, damp sites. High humidity from Lake Michigan is also a likely contributing factor in their occurrence on these relatively exposed, well-drained sites. The presence of large stumps indicates the potential for mature forest development throughout much of the area. We discovered a mature forest which represents the final stages of succession on Michigan dunes. We can point to the development of a type of mesophytic forest with a rich spring flora and a varied understory which is not likely exceeded elsewhere in the state.

Grand Mere Lakes Area

A general review of the Grand Mere region, including aspects of its natural history as well as folklore, is contained in a report by the Kalamazoo Nature Center (1973). The geological history of the Grand Mere embayment area was discussed by Tague (1947). Vegetation and plant community characteristics of selected areas of Berrien County's Lake Michigan shore were reported earlier by the authors (1979a, 1979b).

The name "grand mere" seems to have been derived from "grand marais," meaning big swamp. Although swamp forest covers much of the area under consideration, other habitats include dune, fen, upland forest, and small lakes. One distinct difference between the Grand Mere Lakes area and other parts of the embayment is the predominance of swamps and wetland habitats which are for the most part lacking in adjacent dune localities. The wetter sites make possible

a number of entirely different ecological communities varying from the aquatic vegetation in the three small lakes to that of their boggy borders beyond which lies swamp forest.

The Grand Mere embayment is a lowland located in western Berrien Co. approximately 1.6 km (1 mi) wide by 26 km (16 mi) in length. It extends from the village of Lakeside northward to Glenlord Road which is about 2.7 km (1.7 mi) north of North Grand Mere Lake. The area was inundated by the waters of the Glenwood stage of Lake Chicago—a postglacial lake formed as the Wisconsin glacier retreated northward and its meltwater filled the southern end of the Lake Michigan basin. Water elevation at this stage was 195 m (640 ft) (Dorr & Eschman, 1970). Various postglacial lakes eroded extensive quantities of glacial till along Lake Michigan separating out the sand which was blown by the prevailing westerlies into dunes. Today in the embayment system are dunes—some more than 10,000 years in age with elevation exceeding 213 m (700 ft). Shore features of several lake stages remain. A narrow border of low dunes separates North and Middle Grand Mere Lakes from Lake Michigan. In the southwest sector of the lakes area is a large triangular portion occupied by an extensive system of large dunes derived from Algonquin, Algoma, and Nipissing Lake stages.

Over the centuries a rich forest cover has developed in protected areas. Oak woodlands now cover many high dunes. In steep-sided valleys mesic forests of beech, sugar maple, and hemlock are found. Of special interest is the mixture of northern and southern elements of vegetation. Such a rich mixture is not found in dunes farther north. In other nearby dunes areas wind action has hampered forest development, and large areas of open sand remain.

The South, Middle, and North Grand Mere Lakes (Fig. 8) are situated approximately in the center of the embayment area. Water in these connecting lakes flows northward emptying into Lake Michigan from the west side of North Lake. South Lake's elevation is 178 m (584 ft), or 1 m (3 ft) above the approximate mean level of Lake Michigan.

West of South and Middle Lakes extensive open dunes are found. However, the great majority of dunes in this locality are forested although mesic conditions found elsewhere are, for the most part, lacking here. Except for the paucity of conifers, the integrity of the forest structure seems to have been preserved.

A shallow dune valley, shown in Fig. 9, lies in a section of open terrain not far from Lake Michigan. The area, having a slope of approximately 10° to the west, was partially covered with dune species typical of the region. There were no trees and only a few scattered shrubs—sand cherry and wafer ash (*Ptelea trifolia*). The ground cover consisted primarily of little bluestem grass (*Andropogon scoparius*) and sand reed-grass (*Calamovilfa longifolia*) mixed with beach wormwood (*Artemisia caudata*), Canada wild-rye (*Elymus canadensis*), and beach grass. Small coverage was provided by bouncing bet (*Saponaria officinalis*), dune goldenrod (*Solidago spathulata*), and seaside-spurge (*Euphorbia polygonifolia*). Of limited occurrence were evening primrose (*Oenothera biennis*) and sea rocket (*Cakile edentula*). The present community structure in this site

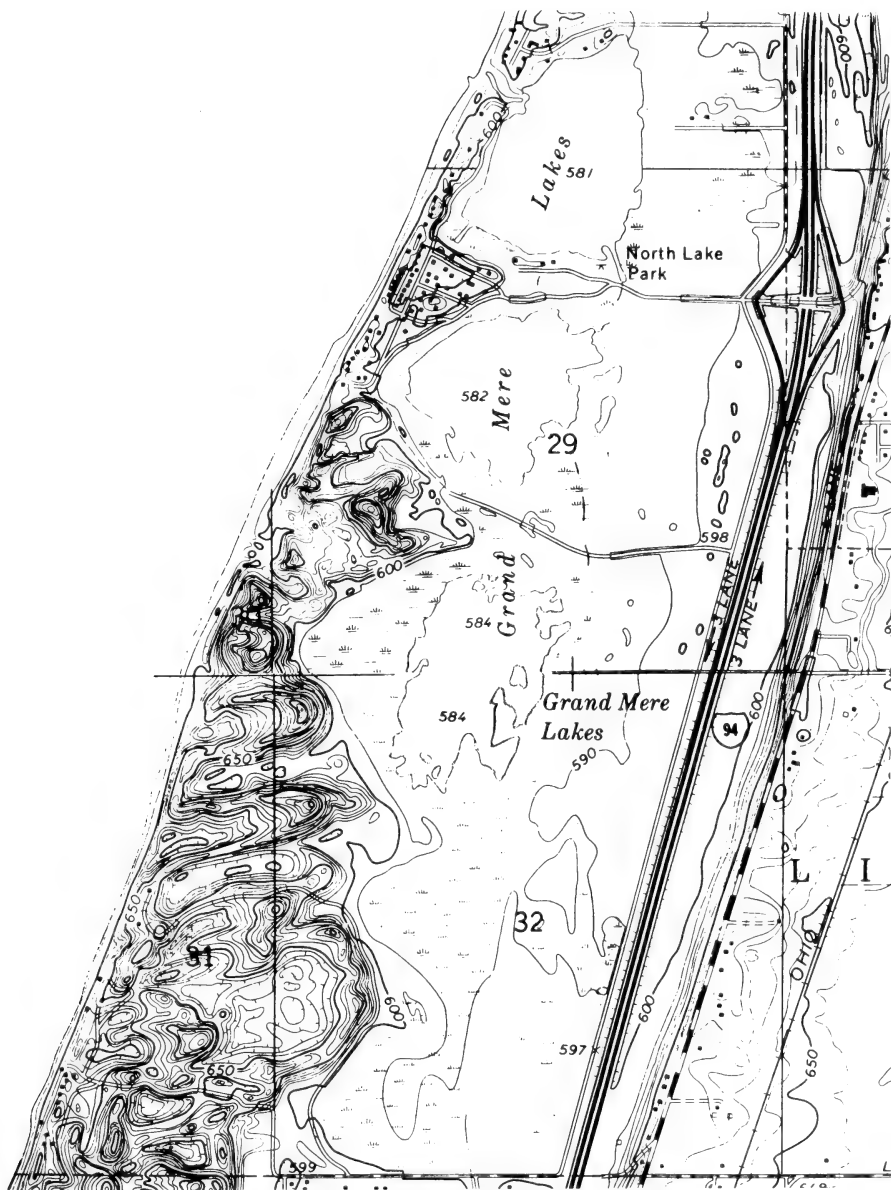


Fig. 8. Contour map of Grand Mere Lakes area (USGS quadrangles Bridgman, Stevensville). Scale: 11 cm (4.3 in.) = 1.6 km (1 mi.).



Fig. 9. West-facing view of open dunes of the Grand Mere Lakes area. Photographed Aug. 14, 1980.

is expected to remain essentially unchanged as long as shifting sand conditions prevail.

We noted destruction which threatens the morphology and integrity of dunes. Dune buggies, off-road vehicles, and heavy foot traffic rupture the binding stems and roots that provide most of the sand-stabilizing capacity of the vegetation (Fig. 10). These tracks can lead to the creation of "wind tunnel" formations (Fig. 11). However, erosion also occurs from natural causes resulting in the destruction of mature forest ecosystems. Figure 12 shows sands of Warren Dunes blown northward into a mature forest burying the lower portion of basswood trees.

Located not far from Lake Michigan was a stand of black walnut trees (*Juglans nigra*), the aspect of which is shown in Fig. 13. This site was adjacent to large open areas dominated by dune grasses. This narrow deep valley was unlike any other we have observed among the sand dunes of Michigan. The black walnut trees may be as old as 50 years. Measurements of DBH for the largest trees, cm (in), were as follows:

39.8(15.7)	22.2(8.7)	12.5(4.9)
25.5(10.0)	18.1(7.1)	11.0(4.3)
24.6 (9.7)	15.5(6.1)	10.8(4.3)
24.6 (9.7)	13.7(5.4)	8.6(3.4)
		8.4(3.3)

The presence of this impressive stand of trees upon very sandy soil perhaps bears witness to the moisture of winds which blow inland from Lake Michigan. We noted that the trunks were covered by lichens which may be indicative of high humidity. Relative humidity data from the nearest station, Muskegon, indicate between 64% and 81% over an 18-year period (U.S. Dept. Comm., NOAA, 1978).

In the shrub layer wafer ash dominated although associates were bitter-sweet (*Celastrus scandens*), common greenbrier (*Smilax rotundifolia*), choke cherry (*Prunus virginiana*), and river-bank grape (*Vitis riparia*). Also present were several seedlings of black walnut.

The ground cover was mostly of wild bergamot (*Monarda fistulosa*), with poison ivy (*Rhus radicans*), bouncing bet, and starry false Solomon's-seal (*Smilacina stellata*) supplying appreciable amounts of cover. Other common species were giant goldenrod (*Solidago gigantea*), showy goldenrod (*S. speciosa*), Canada wild-rye (*Elymus canadensis*), little bluestem, Canada bluegrass (*Poa compressa*), and Virginia creeper (*Parthenocissus quinquefolia*). Present to a less degree were spiderwort (*Tradescantia ohioensis*), puccoon (*Lithospermum carolinense*), and carrion-flower (*Smilax lasioneura*).

To sample swamp forest vegetation a quadrat was laid out in a mature woodland just west of Thornton Rd. about 0.1 mile south of Grand Mere Rd. The relative dominance of canopy trees, based on basal area measurements (Table 1, plot 1), was as follows: basswood (*Tilia americana*) 44%, tulip-tree



Fig. 10. Mt. Edward blowout as viewed from the shore of Lake Michigan. Note path formation due to heavy traffic. Photographed May 15, 1979.



Fig. 11. Erosion of dune surface due to off-road vehicle traffic. Marram grass is the principal dune-binding species. Photographed July 18, 1979.

(*Liriodendron tulipifera*) 27%, sugar maple (*Acer saccharum*) 11%, and white ash (*Fraxinus americana*) 9%. Species furnishing little coverage were red maple (*Acer rubrum*), blue beech (*Carpinus caroliniana*), black ash (*Fraxinus nigra*), American elm (*Ulmus americana*), hop hornbeam (*Ostrya virginiana*), flowering dogwood (*Cornus florida*), and papaw (*Asimina triloba*). We noted evidence of fire on tree stumps near the study quadrat.

The shrub layer was impressively dominated by spice bush (*Lindera benzoin*), with a considerable amount of white ash, blue beech, and papaw. Other species showing appreciable cover were white ash, as well as choke cherry, witch hazel (*Hamamelis virginiana*), and sugar maple. Other woody species present in small numbers included black ash (*Fraxinus nigra*), red maple, red oak (*Quercus borealis*), flowering dogwood, gray dogwood (*Cornus racemosa*), alternate-leaved dogwood (*C. alternifolia*), sassafras (*Sassafras albidum*), japanese barberry (*Berberis thunbergii*), common elder (*Sambucus canadensis*), swamp rose (*Rosa palustris*), river-bank grape, bristly greenbrier (*Smilax tamnoides*), and maple-leaved viburnum (*Viburnum acerifolium*). Woody plant totals were 11 species of trees measured for DBH and 22 species of understory plants. Among the tree species measured, five, namely, black ash, hop hornbeam, tulip-tree, basswood (*Tilia americana*), and red maple, were not found among the understory.

Among ground cover species Virginia creeper and black snakeroot (*Sanicula marilandica*) were most abundant, each having about 10–15% cover-



Fig. 12. Migration of wind-blown sand into mature forest of Warren dune covering lower portion of basswood trees. Photographed June 12, 1979.



Fig. 13. Aspect of black walnut stand in dune pocket. Photographed June 26, 1980.

age. False Solomon's-seal, large white trillium (*Trillium grandiflorum*), Canada mayflower (*Maianthemum canadense*), and blue-stemmed goldenrod (*Solidago caesia*) were numerous, but their cover was each less than 5%. A number of species with only small coverage included jack-in-the-pulpit (*Arisaema triphyllum*), starry false Solomon's-seal, sedges (*Carex* spp.), hairy Solomon's-seal (*Polygonatum pubescens*), wild sarsaparilla (*Aralia nudicaulis*), arrow-leaved aster (*Aster sagittifolius*), swamp goldenrod (*Solidago patula*), violets (*Viola* spp.), running strawberry-bush (*Euonymus obovatus*), field horsetail (*Equisetum arvense*), white lettuce (*Prenanthes alba*), poison ivy, bellwort (*Uvularia grandiflora*), woodland knotweed (*Polygonum virginianum*), lady fern (*Athyrium filix-femina*), bottlebrush grass (*Hystrix patula*), dwarf raspberry (*Rubus pubescens*), and pointed tick trefoil (*Desmodium glutinosum*).

For an example of a mixed hardwood forest type we established a quadrat on a low, sandy ridge west of Thornton Rd. approximately 1.1 km (0.7 mi) south of Grand Mere Rd. Almost a third of the tree basal area consisted of red maple (Table 1, plot 2) with about 20% each supplied by white oak (*Quercus alba*) and black oak (*Q. velutina*). We noted 14% sassafras and 12% beech (*Fagus grandifolia*), as well as a small amount of hop hornbeam. Since this stand contained species characteristic of drier habitats as well as those typical of less well-drained sites, the term "mixed hardwood" seemed an appropriate characterization.

The principal shrub cover consisted of maple-leaved viburnum, witch hazel, common greenbrier, black oak, sassafras, and white ash. Also occurring

were a number of seedlings of red maple and tulip-tree as well as some common blackberry (*Rubus allegheniensis*), low blueberry (*Vaccinium ?brittonii*), and hop hornbeam. A total of 19 species of trees and shrubs were noted in the study plot.

The ground cover with 20 species was diverse but not dense. The principal species consisted of bracken (*Pteridium aquilinum*), blue-stemmed goldenrod, and wintergreen (*Gaultheria procumbens*), all with less than 5% coverage. Other species with only small coverage were false Solomon's-seal (*Smilacina racemosa*), Pennsylvania sedge (*Carex pensylvanica*), running strawberry-bush, and Virginia creeper. Even less abundant were such plants as Canada mayflower, large-leaved aster (*Aster macrophyllus*), hairy Solomon's-seal, elliptic shinleaf (*Pyrola elliptica*), large white trillium, beech-drops (*Epifagus virginiana*), white lettuce, long-spurred violet (*Viola rostrata*), partridge-berry (*Mitchella repens*), sweet cicely (*Osmorhiza claytoni*), and royal fern (*Osmunda regalis*).

One of the more unusual plant habitats in the Grand Mere sector was a small wet prairie located just south of Grand Mere Rd. The open meadow shown in Fig. 14 was surrounded by swamp forest and dominated by big bluestem grass (*Andropogon gerardi*) and composites such as tall coreopsis (*Coreopsis tripteris*), Missouri ironweed (*Vernonia missurica*), black-eyed Susan (*Rudbeckia hirta*), goldenrods including tall, Canada, grass-leaved, giant, bog, gray, and rough goldenrods (*Solidago altissima*, *S. canadensis*, *S. graminifolia*, *S. gigantea*, *S. uliginosa*, *S. nemoralis*, and *S. rugosa*), and flat-top, heath and rush asters (*Aster*



Fig. 14. View of wet prairie east of Middle Lake. Photographed Aug. 13, 1980.

umbellatus, *A. ericoides*, and *A. junciformis*). We also noted in large numbers Joe-Pye weed (*Eupatorium maculatum*) and boneset (*E. perfoliatum*), woodland and tall sunflower (*Helianthus divaricatus* and *H. giganteus*), pussy toes (*Antennaria plantaginifolia*), daisy fleabane (*Erigeron strigosus*), and marsh fern (*Thelypteris palustris*). Of special interest was the large number of marsh pinks (*Sabatia angularis*—Fig. 14, lower right), a species on Michigan's rare, endangered and threatened list (Wagner et al., 1977). Another uncommon plant found in this habitat was stiff yellow flax (*Linum striatum*). Common plants here included swamp rose, as well as such grasses as redtop (*Agrostis gigantea*), Canada blue grass, and switch grass (*Panicum virgatum*). This wet prairie also contained wild carrot (*Daucus carota*), indian hemp (*Apocynum sibiricum*), purple meadow-rue (*Thalictrum dasycarpum*), strawberry (*Fragaria virginiana*), showy and Dillenius' tick trefoil (*Desmodium canadense*, and *D. dillenii*), self-heal (*Prunella vulgaris*), wood betony (*Pedicularis canadensis*), wild bergamot, Canada anemone (*Anemone canadensis*), and thimbleweed (*A. virginiana*).

Along the edge of the prairie we found red maple, speckled alder (*Alnus rugosa*), red osier, silky dogwood (*Cornus purpurea*), northern dewberry (*Rubus flagellaris*), cockspur hawthorn (*Crataegus crus-galli*), and bittersweet.

A lowland area north of North Lake had vegetation common to fens. In addition to many of the plants found in the wet prairie were shrubby cinquefoil (*Potentilla fruticosa*), cowbane, closed gentian (*Gentiana andrewsii*), Kalm's lobelia (*Lobelia kalmii*), wood lily (*Lilium philadelphicum*), Riddell's goldenrod (*Solidago riddellii*), ground-nut (*Apios americana*), cordgrass (*Spartina pectinata*), and grass-of-Parnassus (*Parnassia glauca*).

The three Grand Mere Lakes vary considerably in the development of aquatic vegetation. North Lake (Fig. 8) with a large area of open water is used for sport fishing. Middle Lake possesses large patches of floating and emergent vegetation interspersed with areas of open water, whereas South Lake (Fig. 15, 16) displays large areas of shallow water vegetation and little open water. The west border of South Lake has a wide band of vegetation. A number of years ago a large portion of this area served as a commercial cranberry bog.

Due to lack of time we were not able to sample thoroughly for aquatics, but a number of interesting finds were noted. In our survey of South Lake we noted pitcher-plant (*Sarracenia purpurea*), cranberry (*Vaccinium macrocarpon*), leatherleaf (*Chamaedaphne calyculata*) and marsh St. John's-wort (*Triadenum virginicum*). Hummocks here support water willow (*Decodon verticillatus*), buttonbush (*Cephalanthus occidentalis*), swamp rose, and occasionally speckled alder. We collected for the first time humped bladderwort (*Utricularia gibba*) and knotted spike-rush (*Eleocharis equisetoides*).

Floating vegetation in the lakes supplied considerable cover consisting primarily of fragrant water lily (*Nymphaea odorata*), yellow water lily (*Nuphar advena*), pickerel-weed (*Pontederia cordata*), water-shield (*Brasenia schreberi*) as well as several species of pondweeds (*Potamogeton*). Large portions of the lake bottom were covered by swaying sedge (*Scirpus subterminalis*), and most stems were not emergent even during September. Emergent species include common cat-tail (*Typha latifolia*), arrow-arum (*Peltandra virginica*), wapato (*Sagittaria latifolia*), water-plantain (*Alisma plantago-aquatica*), small bur-reed

(*Sparganium minimum*), threesquare (*Scirpus americanus*), and species of bulrush (*Scirpus*). We found in South Lake restricted distributions of wild-rice (*Zizania aquatica*) and purple bladderwort (*Utricularia purpurea*).

Among the submerged plants were waterweed (*Elodea canadensis*), tapegrass (*Vallisneria spiralis*), whorled water milfoil (*Myriophyllum verticillatum*), slender naiad (*Najas flexilis*), bladderwort (*Utricularia vulgaris*), and various potamogetons.

The shrubby borders of all the lakes had such species as Michigan holly (*Ilex verticillata*), red osier, silky dogwood, sandbar willow (*Salix interior*), swamp rose, red maple, and American elm. An unusual plant found along the north edge of Middle Lake was rose mallow (*Hibiscus palustris*).

About 1.6 km (1 mi) south of South Grand Mere Lake a mature black oak forest covered the steep banks of large dunes at the eastern border of the dune complex in the northern 1/4 of Sec. 6, T6S, R19W. This forested area (slope 27° east) is a portion of the dune system associated with post-glacial Lake Algonquin dating back some 9,000 years. Sand dunes of this age are uncommon in Michigan; most of the large dune complexes being formed during the Nipissing stage about 3,500 years ago. This pre-climax oak forest is a successional stage typical of considerable portions of forested dunes along the southeastern borders of Lake Michigan. Data collected from the study quadrat (Table 1, plot 3) illustrates the overwhelming dominance of black oak which supplies over 93% of the stem basal area for the plot. The balance of the coverage (7%) was fur-



Fig. 15. East-facing view of South Lake showing bog mat along its west border and dune forest in foreground. Photographed May 16, 1979.



Fig. 16. West-facing view of South Lake as seen from lake level. Hummocks of vegetation provide unique habitats in this locality. Photographed Sept. 24, 1980.

nished by white oak. Adjoining areas contained tulip-tree and sassafras. Common understory species were witch hazel, maple-leaved viburnum, sassafras, flowering dogwood, common greenbrier, and blueberry. Where the canopy was more open, common greenbrier formed dense thickets. Other understory plants in the study plot were red oak, beech, red maple, common juniper, river-bank grape, and shadbush (*Amelanchier* sp.). The ground cover was sparse although several common species, including Pennsylvania sedge, wintergreen, bracken, false Solomon's-seal, blue-stemmed goldenrod, and hair-cap moss (*Polytrichum* sp.), were observed.

We have used the term "heath bald" to characterize an unforested part of a dune dominated by shrubs 75% of which were huckleberry (*Gaylussacia baccata*) and 25% low blueberry (*Vaccinium angustifolium*). This area, located near the previously described black oak forest, was recently destroyed by sand mining. At this site (Fig. 17) were a few isolated saplings of sassafras, witch hazel, black oak, and shadbush in addition to pasture rose (*Rosa carolina*) and common greenbrier. Other scattered species were bracken, Virginia creeper, and frostweed (*Helianthemum canadense*). This heath area was approximately 100 m² in area, although the very dense assemblage of the shrub heath and the paucity of canopy layer and ground cover rendered a unique aspect for sand dunes vegetation. We have seen very few such plant associations in Michigan.

Mt. Edward Area

The map (Fig. 18) shows in outline a study site of 104 ha (258 acres) comprising the most of Sec. 24, T6S, R20W. It is bordered on the west by Lake Michigan and on the east by Highway I-94 at the Bridgman interchange. The northern and southern borders have been extensively modified by dune removal in the Weko Beach area and by the construction of residences. The area encompasses the Mt. Edward dune blowout located in the southwest sector (Fig. 18, stippled), and three ponds (black areas on the map) are located along the eastern border. In the northwest part of the study site is a small stream, Tanner Creek (represented by the heavy curved line in the upper left part of Fig. 18).

Disturbance in the southeastern portion of the tract has resulted in some 20 acres being stripped of all plant cover (Fig. 19) to begin sand mining. Fire-marked stumps were scattered throughout the area, but several stands of large trees, e.g., DBH 46 cm (18 in) to 61 cm (24 in), bore witness to otherwise undisturbed conditions in recent decades. The Mt. Edward tract is unlike any other in the world in terms of overlap of northern and southern floristic components, richness of flora, occurrence of rare, endangered, and threatened plants, and antiquity of dune forests.

Altitudinal variation ranges from approximately 244 m (800 ft) at the summit of Mt. Edward blowout (Fig. 10) to the elevation of Lake Michigan at 177 m (580 ft). The terrain is comprised of Nipissing, Algoma, and Algonquin



Fig. 17. View of the "heath bald" showing an almost pure stand of huckleberry and blueberry. Photographed May 15, 1979.

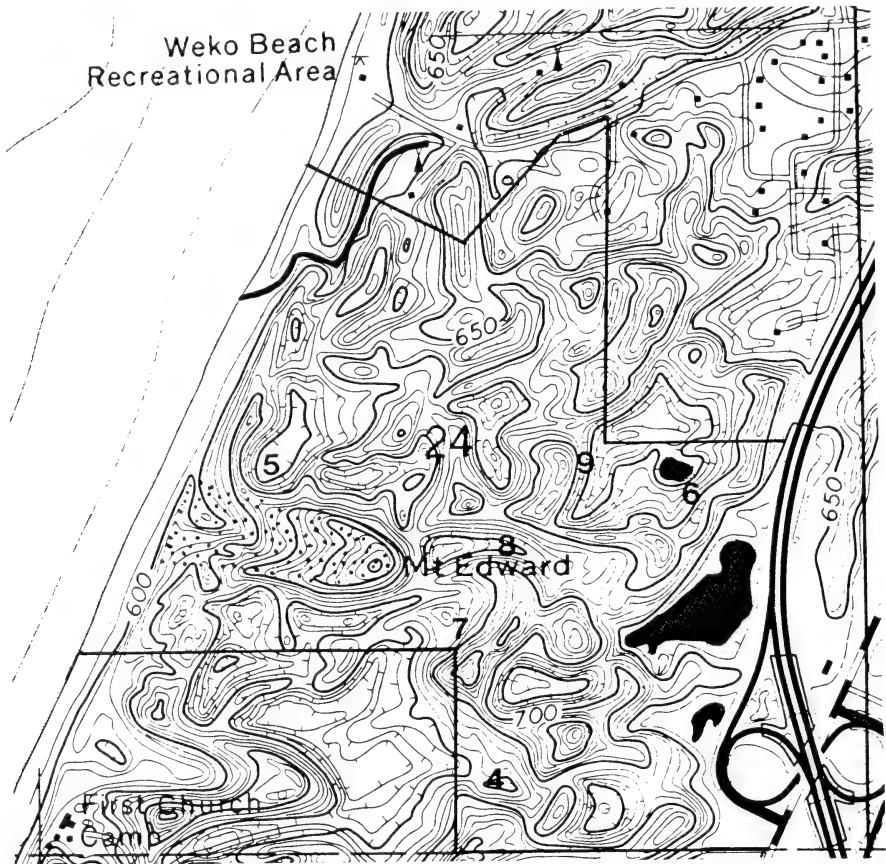


Fig. 18. Contour map of Mt. Edward study site showing three ponds (blackened) and dune blowout (stippled). (USGS Bridgman quadrangle.) Scale 16.5 cm (6.5 in.) = 1.6 km (1 mi.)

dunes (Fig. 6). The Algonquin dunes located in the eastern sector are about 11,500 years in age. (Portions in this section have been mined.) Slopes are steep (up to 30°), and dune ridges may surpass 30 m (110 ft) as far as 1.6 km (1 mi) inland. This rugged topography, together with variation in exposure, helps create mesic habitats.

A rich mesic forest was located in the southeastern section of the tract directly west of the sand mining area. The location of this quadrat is indicated by a "4" on the map (Fig. 18). The test plot was relatively flat with more than one-half of the coverage supplied by beech, one-quarter by basswood, and one-fifth by hemlock (Table 1, plot 4). Although no sugar maple trees were located on the plot, this species was present in adjacent areas, as well as in the understory. The presence of sugar maple at various stages of maturity indicated the mesic character of the adjacent area.

Principal understory species included sugar maple, sassafras, flowering dogwood, white ash, hop hornbeam, maple-leaved viburnum, witch hazel, hemlock (*Tsuga canadensis*), bitternut hickory (*Carya cordiformis*), chestnut oak (*Quercus muhlenbergii*), and basswood. Present in lesser amounts were beech, leatherwood, choke cherry (*Prunus virginiana*), fly honeysuckle (*Lonicera canadensis*), and hazel (*Corylus americana*).

The ground cover was comprised of 65 species within the 20 m² quadrat. Most of the cover species were common spring flora elements such as large white trillium, blunt-lobed hepatica (*Hepatica americana*), bellwort, columbine (*Aquilegia canadensis*), white baneberry (*Actaea alba*), mayapple (*Podophyllum peltatum*), large-leaved aster, partridge berry, Pennsylvania sedge, running strawberry-bush, maidenhair fern (*Adiantum pedatum*), marginal shield-fern (*Dryopteris marginalis*), hairy Solomon's-seal, false Solomon's-seal, and bishop's-cap (*Mitella diphylla*). Plants of particular interest were spotted wintergreen (*Chimaphila maculata*), ginseng (*Panax quinquefolia*), and bracted orchid (*Habenaria viridis*). Less than 10 m from the plot we observed allegheny vine (*Adlumia fungosa*). It is extremely unusual to find at one such small locality as many as three plants on Michigan's list of rare, endangered, and threatened plants!

An increment core sample was taken from a nearby hemlock. The tree was 33 m (109 ft) in height, the DBH was 57 cm (23 in), and the crown spread 12.8 m (42 ft); it was at least 224 years old. On the basis of our experience elsewhere



Fig. 19. Sand dune in the Bridgman site stripped of vegetation in preparation for mining. Photographed July 17, 1979.

we estimate that at least 1,000 years are required to achieve conditions leading to forest development such as that witnessed here.

A very deep valley lies just over the first landward high dune and just north of the Mt. Edward blowout. Its location is indicated by the numeral "5" in Fig. 18. The richness of the vegetation and size of the trees suggest the virgin character of the forest (Fig. 20). A quadrat was set up on the relatively flat valley floor in the southern portion of the valley. Coverage values (Table 1, plot 5) show that yellow birch (*Betula allegheniensis*), basswood, and tulip-tree predominate. Smaller amounts of coverage were provided by sugar maple, white ash, and sassafras. Adjoining areas showed considerable beech, sugar maple, hemlock, and red oak, all of which indicate the mesic character of this forest.

Understory species included hop hornbeam, blue beech, basswood, white ash, and sassafras, although spice bush and sugar maple saplings were more conspicuous. Virginia creeper provided the greatest coverage among ground cover species in the quadrat, but the whole area was carpeted with a rich and diverse assemblage of spring wildflowers (over 40 species). Notable constituents of the ground cover were wild leek (*Allium tricoccum*), Canada mayflower, jack-in-the-pulpit, early meadow-rue (*Thalictrum dioicum*), blunt-lobed hepatica, and white lettuce.

Many very large trees were scattered throughout the valley. The DBH, cm (in), of several larger ones appears below:

basswood	56(22), 66(26), 84(33)-dead tree	sugar maple	63(25)
beech	50(20), 54(21), 62(25), 94(37)	tulip-tree	62(24), 77(30)
hemlock	57(23), 66(26)	white ash	44(17)
red oak	72(29), 83(33)	white pine	49(19)
		yellow birch	82(32)

Directly east of this valley was a long, narrow valley of similar character. We recorded the height of one tulip-tree, 37 m (121 ft), a height typical of other trees in this locality. A series of DBH measurements were made in this second valley as follows, DBH = cm (in):

basswood	92(36)	hop hornbeam	23(9)
beech	53(21), 58(23), 60(24)	red oak	50(20)
hemlock	62(25), 81(32)	sugar maple	51(20), 65(26), 89(35)
		tulip-tree	88(32)

An area of special interest was located in the deep valley on the south side of the northernmost "hemlock pond" indicated by the numeral "6" on Fig. 18. At least a dozen large hemlocks dominated the area, but beech is also present (Fig. 21 & Table 1, plot 6). This habitat was located between two impressive Algonquin ridges over 100 ft in height and near a very strong Nipissing ridge. There was thus considerable protection for the hemlock trees which were situated, for the most part, near the southeast end of the pond. Hemlock thrives best where humid conditions prevail, and at this site was the largest concentration of the species on the tract.

As typical of large hemlock stands, the understory development was minimal. This locality reminds one of a more northern forest type. This impres-



Fig. 20. Virgin forest north of Mt. Edward blowout showing (left to right) large sassafras, white oak, and yellow birch. Photographed June 13, 1979.



Fig. 21. Mature hemlock and beech stand along the south side of "north (hemlock) pond." Photographed Aug. 30, 1979.

sion was enhanced by the presence of goldthread (*Coptis trifolia*), starflower (*Trientalis borealis*), and rattlesnake-plantain (*Goodyera pubescens*), all elements of Michigan's boreal flora. Of interest was the presence of more than 30 plants of spotted wintergreen. Canada mayflower was the principal ground cover species.

Large trees measured in the locality were as follows, DBH = cm (in):

beech	51(20), 52(20), 52(20), 57(23), 62(25), 72(28)-dead	red maple	56(22)
black gum	42(17)	red oak	68(27)
hemlock	50(20), 51(20), 56(22), 57(23), 57(23), 57(23), 65(26), 66(26)	tulip-tree	46(18), 53(21)
		white pine	97(39)

Age estimates based upon increment cores samples and size data were taken on two trees at the hemlock pond site, as follows:

	height m (ft)	spread m (ft)	diameter cm (in)	est. age (yrs)
hemlock	34(110)	13(44)	56(22)	158
tulip-tree	36(119)	14(47)	53(21)	77

The Mt. Edward area possessed a number of very deep interdunal valleys; the location of one of these is indicated by the number "7" on Fig. 18. Its understory was unusually well developed. A quadrat, set up on the valley floor,

showed coverage by dominant trees approximately 30% sugar maple, 15% basswood, and 11% red oak (Table 1, plot 7).

The greatest coverage of the dense understory was by spice bush, with substantial amounts of sugar maple, hop hornbeam, blue beech, papaw, sassafras, and leatherwood. Minor coverage came from maple-leaved viburnum, white ash, and common greenbrier. Ground cover was less well developed here than in other wooded sites due to the greater understory development which prevents much of the light from penetrating to the forest floor. The cover species were bloodroot (*Sanguinaria canadensis*), Virginia creeper, bellwort, running strawberry-bush, blue-stemmed goldenrod, false Solomon's-seal, wild sarsaparilla, and mayapple.

On Fig. 18, the numeral "8" shows the location of a 30° north-facing slope of one of the deep valleys of the Mt. Edward tract. In the study plot (Table 1, plot 8), almost 65% of the coverage was from basswood, 24% from hemlock, and about 10% from sugar maple, with a small amount from beech. These dominants indicate the mesic character of the forest. With very heavy shade, the understory was quite sparse. Spice bush provided considerable coverage, along with saplings of sugar maple. Ground cover was principally due to Virginia creeper and marginal shield fern. The fact that Jack-in-the-pulpit was common indicates the high moisture effectiveness of the heavily shaded slope. A number of common spring wildflowers were noted.

Plot 9 (Fig. 18) was located just east of the center of section 24 on a slope inclined 30° to the east. As the data in Table 1 show, red oak was dominant with a 56% basal area coverage. Plot 8 just discussed, with the same amount of slope but to the north, was dominated by basswood and hemlock. Another notable difference between plots 8 and 9 was the presence on the latter of sassafras, tulip-tree, and black cherry. These cove-like pocket areas seemed ideal for the study of exposure effects on development of forest vegetation in what is likely very similar soil conditions. Approximately 20 species were noted in the understory, dominants being sassafras, sugar maple, spice bush, flowering dogwood, and hop hornbeam. Ground cover included a number of spring flora species among which were bloodroot, bellwort, violets, large white trillium, false Solomon's-seal, and hairy Solomon's-seal. Ferns included Christmas fern, ebony spleenwort, marginal shield-fern, and bracken. Spotted wintergreen was growing near this site.

Mt. Edward ranks among the higher dunes, reaching an elevation over 244 m (800 ft). The blowout (Fig. 10) consists of a long channel cut by wind action through the high barrier dune ridge that flanks the shore of Lake Michigan. Wind action has left a large area of open sand extending from a low point near the lake front to a high point some 610 m (2,000 ft) inland.

Sand moving up the pinnacle has covered most of a large group of cottonwood trees (Fig. 10, center background). North of these trees (in Fig. 10 to the left of the cottonwood trees) was a clone of red osier, a species often associated with aquatic sites. Its presence here suggests that ecotypes may have evolved in this region over the centuries.

Throughout the blowout were found common dune plants, such as sand reed grass, broom sedge, sand cherry, puccoon (*Lithospermum carolinense*),

green milkweed (*Acerates hirtella*), dune goldenrod, flowering spurge (*Euphorbia corollata*), seaside-spurge (*E. polygonifolia*), Pitcher's thistle (*Cirsium pitcheri*), bugseed (*Corispermum hyssopifolium*), sand cress (*Arabis lyrata*), beach wormwood (*Artemisia caudata*), and butterfly-weed (*Asclepias tuberosa*).

The low area (Fig. 10, center foreground) contained willow (*Salix* sp.) and rushes (*Juncus* sp.). Ponding of water occurs here after rainfall. Along the southwestern edge of the blowout was a small stand of white pine (*Pinus strobus*). Characteristic plants occurring with the pine were Canada yew (*Taxus canadensis*) and bearberry (*Arctostaphylos uva-ursi*).

Along the eastern border of the study area were three ponds whose location is shown in Fig. 18. These ponds are not borrow pits created during the 1963 construction of I-94 highway; older maps show their presence, although water table and drainage phenomena may have been modified to a degree by highway construction. The small, north pond, bordered by hemlock and designated "hemlock pond," was discussed above. The two remaining ponds border I-94; the larger we term "north pond" (Fig. 22) and the southernmost "south pond." Since many dune systems lack adjacent small bodies of water these areas were of special interest.

"North pond" was bordered for three-quarters of its perimeter by trees, some of which may exceed 200 years in age. Common species along its border were black and white oak, black gum (*Nyssa sylvatica*), and tulip-tree, with high-bush blueberry (*Vaccinium corymbosum*) as an occasional understory border shrub. A tulip-tree on the south shore had a DBH of 48 cm (19 in), and a black gum's DBH was 52 cm (20 in). Black gum was a common tree along the northwest border—one measuring 38 cm (15 in) DBH. Examples of the size of large oaks was the DBH of 90 cm (35 in) for a white oak, while a black oak on a nearby ridge had a DBH of 88 cm (35 in). Along the southwest corner of the pond was a habitat not found elsewhere except at the small pond to the south. The stand of trees at this location was an interesting mixture of mesic and swamp forest types whose sizes were as follows DBH = cm (in):

beech	19(8)	red maple	62(25)
black gum	35(14), 38(15), 40(16), 53(20)	red oak	57(23)

Other trees of interest here were sugar maple, hemlock, and sassafras. Mixed with high-bush blueberry were Michigan holly (*Ilex verticillata*), witch hazel, flowering dogwood (*Cornus florida*), and shadbush (*Amelanchier* sp.). Both cinnamon fern (*Osmunda cinnamomea*) and royal fern (*O. regalis*) were common. In the ground cover layer were wintergreen (*Gaultheria procumbens*), partridge-berry (*Mitchella repens*), and Canada mayflower. Other species include indian cucumber-root (*Medeola virginiana*), wild sarsaparilla (*Aralia nudicaulis*), indian pipe (*Monotropa uniflora*), cowwheat (*Melampyrum lineare*), and spotted wintergreen. A huge stand of Virginia chain fern (*Woodwardia virginica*) covered much of the pond's surface. A fringe of buttonbush (*Cephalanthus occidentalis*) extended around the shallow water border (Fig. 22), along with some Michigan holly.



Fig. 22. South-facing view of "north pond" showing black gum trees and buttonbush in the water. Photographed May 16, 1979.

"South pond" had a large coverage of buttonbush, willows, and Michigan holly. Of interest in the southeast portion of the pond was a large colony of lizard's tail (*Saururus cernuus*), uncommon in Michigan but more common in the southeastern U.S. Along the northern border of the pond was a row of 41 black gum trees, two of which had DBH measurements of 25 cm (10 in). The border also contained yellow birch and beech as well as a white oak whose DBH measured 83 cm (33 in).

A small stream, Tanner Creek, is located in the northwest corner of the site (Fig. 18, heavy curved line). The stream enters the area from the north and flows through a narrow wooded valley. Observations were made at a point where the stream turns to the west toward Lake Michigan. Forest composition is indicated by the sizes of some representative trees, DBH = cm (in):

basswood	35(14), 43(17), 52(21)	hemlock	50(20)
blue beech	20(8)	sugar maple	24(10), 25(10)
		white pine	43(17)

Understory shrubs consisted of alternate-leaved dogwood (*Cornus alternifolia*) and spice bush as well as saplings of sugar maple, white ash, sassafras, and hemlock. Typical of the ground cover species were blunt-lobed hepatica, large white trillium, starry false Solomon's-seal, wood betony (*Pedicularis canadensis*), Canada mayflower, early meadow-rue (*Thalictrum dioicum*), bishop's-cap, and marginal shield-fern. Other species included running strawberry-bush, lance-leaved bedstraw (*Galium lanceolatum*), touch-me-not (*Impatiens biflora*), part-ridge berry, large-leaved aster, hog-peanut (*Amphicarpa bracteata*), and rattle-snake fern (*Botrychium virginianum*).

FLORISTICS

More than 600 species of vascular plants occurred in the sites discussed. Among these, eight are on the Michigan rare, endangered, and threatened plant list (Wagner et al., 1977). Pitcher's thistle (*Cirsium pitcheri*) and ginseng (*Panax quinquefolius*) are threatened in Michigan as well as in the U.S. (Ayensu & DeFilipps, 1978). Other species listed as threatened in Michigan are wild-rice (*Zizania aquatica*), marsh pink (*Sabatia angularis*), rose mallow (*Hibiscus palustris*), and broad-leaved sedge (*Carex platyphylla*). Michigan rare plants found here include allegheny vine and red mulberry (*Morus rubra*).

Among the monocots, we collected specimens of 11 plants not listed for Berrien Co. in Voss (1972): small bur-reed (*Sparganium minimum*), grass-leaved pondweed (*Potamogeton gramineus*), common pondweed (*P. natans*), stiff pondweed (*P. strictifolius*), knee grass (*Panicum dichotomoflorum*), water sedge (*Carex aquatilis*), knotted spike-rush (*Eleocharis equisetoides*), swaying rush (*Scirpus subterminalis*), duckweed (*Lemna minor*), water-meal (*Wolffia columbiana*), and hooded ladies'-tresses (*Spiranthes romanzoffiana*).

Dicots not previously listed for Berrien Co. (Swink & Wilhelm, 1979) were balsam poplar (*Populus balsamifera*), fragrant water lily (*Nymphaea odorata*), bristly buttercup (*Ranunculus pensylvanicus*), pale corydalis (*Corydalis*

sempervirens), American mountain ash (*Sorbus americana*), Dillenius' tick trefoil (*Desmodium dillenii*), ridge-seeded spurge (*Euphorbia glyptosperma*), nodding spurge (*E. preslii*), orange grass (*Hypericum gentianoides*), marsh St. John's-wort (*Triadenum fraseri*), glandular willow-herb (*Epilobium glandulosum*), privet (*Ligustrum vulgare*), bugleweed (*Lycopus virginicus*), humped bladderwort (*Utricularia gibba*), tartarian honeysuckle (*Lonicera tatarica*), and glossy-leaved aster (*Aster lucidulus*). Uncommon dicots included stiff yellow flax (*Linum striatum*) and showy black-eyed Susan (*Rudbeckia fulgida*). Additional work in the region would likely result in the addition of still other novelties for southwestern Michigan. The small ponds and lakes themselves should inspire further search.

CONCLUSION

The dunes of Berrien Co. have special significance to students of glacial geology. Found here are beaches, spits, bars, and wave-cut bluffs associated with glacial lakes in the embayment. The area is particularly characterized by its rugged topography which results in very deep valleys. It is under these conditions where rich mesic forest vegetation develops, as evidenced by the existence of virgin forest stands in some of these relatively inaccessible pockets. Of particular interest are several types of wetlands in the Grand Mere Lakes sector that



Fig. 23. Lake Michigan dune bluff showing sandy beach near mouth of Tanner Creek. Note dune forest with tall white pine extending to lake front indicating undisturbed nature of the area. Photographed July 17, 1979.

are lacking in many other dune areas. These wetland sites include shallow lakes and ponds with extensive aquatic flora, bog, fen, and swamp forest. An unusual community is the wet prairie which, in time, may be succeeded by encroachment of the surrounding forest.

Our survey suggests that the large number of plants catalogued for the area, including species on the rare, endangered, and threatened list, can be attributed to the many types of ecological niches that occur here. The co-existence of a number of northern and southern species in this locality is particularly noteworthy. The small dune valley dominated by black walnut trees seems almost a paradox when compared with our observations on other Michigan dunes.

The details of composition of duneland communities discussed herein help point up the uniqueness of the area. These Michigan dunes represent an irreplaceable geological heritage owing to unusual conditions under which they were formed. The barrier dunes along the shore of Lake Michigan (Fig. 23) divert winds off the lake and serve as a protective buffer for inland locations. But more important than their value as buffer agents, they support biotas which have required many centuries for assemblage. An exercise in the ultimate egotism of man would be the destruction of a critical few yet remaining.

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PUBLICATIONS OF INTEREST

- AUTOBIOGRAPHY OF JOHN MACOUN Canadian Explorer and Naturalist 1831–1920. Ed. 2. Ottawa Field-Naturalists' Club Special Publication 1. 1979. xviii + 361 pp. \$10.00. This is a particularly welcome facsimile reprint of the original 1922 autobiography of Canada's great exploring botanist, whose travels included the Great Lakes region as well as proposed railroad routes and other wild portions of North America. A new introduction has been added, in addition to numerous editorial notes, a bibliographical essay, and a very useful index. This fascinating exploratory-biographical narrative is available from the publisher at Box 3264 Postal Station 'C,' Ottawa, Ontario, Canada K1Y 4J5.
- INTERNATIONAL CODE OF NOMENCLATURE FOR CULTIVATED PLANTS—1980. Ed. by C. D. Brickell et al. Regnum Vegetabile 104. 1980. 32 pp. This important document, supplementary to the International Code of Botanical Nomenclature, which governs scientific names, regulates names for cultivars (named horticultural "varieties"—not common names), such as *Syringa vulgaris* 'Mont Blanc' or *S. vulgaris* cv. Mont Blanc. This first new edition of the "cultivated code" since 1969 is available in North America from the American Horticultural Society, Mt. Vernon, Virginia 22121, or the Crop Science Society of America, 677 South Segoe Rd., Madison, Wisconsin 53711, for \$6.25.
- CHECKLIST OF UNITED STATES TREES (NATIVE AND NATURALIZED). By Elbert L. Little, Jr. U. S. Department of Agriculture, Agriculture Handbook 541. 1979. 375 pp. \$10.00. This welcome revision of the very useful 1953 checklist by the same author is basically an alphabetical listing of genera and species by scientific name (with cross-references from synonyms), with common names, synonymy, range, and useful references cited. There are additional notes regarding hybrids and other matters, and references to maps published in the 6-volume *Atlas of United States Trees* (see notice in Mich. Bot. 19: 46. 1980). Among the useful appendices are condensed checklists of scientific and common names, commercial names for lumber, guiding principles for common names, and a botanical index (Englerian sequence) to families and genera. The list accepts 69 naturalized species and about 680 native species, with an original and sensible conservative treatment of *Crataegus*.

THE SNOW TRILLIUM, *TRILLIUM NIVALE*, IN MICHIGAN

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The snow trillium, *T. nivale* Riddell, occurs natively in a narrow band from Pennsylvania to Minnesota (Fernald, 1950). Most of the known populations occur in southern or central Ohio, Indiana, Illinois, and southeastern Minnesota. Outlying colonies are known from Kentucky (Fernald, 1950), Missouri (Steyermark, 1963), Nebraska (Lomasson, 1973), and Michigan. In the eastern part of its range, *T. nivale* is generally very rare or local, but it becomes somewhat more abundant westward. I have been told by knowledgeable local naturalists that the plant is frequent on river bluffs and loess hillsides in the area of Peoria, Illinois. Friends at Rochester, Minnesota, aver that the plant is locally abundant on calcareous soils there and aggressive enough to persist in fencerows after forests are cut. The nearest occurrences to Michigan of sizable populations are in central and west-central Indiana. Deam (1940) mapped the Indiana distribution in 12 counties and reported occurrences in three additional ones.

Beal (1905), in his *Michigan Flora*, reported the snow trillium from Hubbardston, Ionia, Grand Rapids, and Niles and called it rare. I have not seen herbarium vouchers for some of his reports. Emma J. Cole, in her *Grand Rapids Flora* (1901), reported the plant from the banks of Plaster Creek, Paris Township, and woodlands northwest of the city. She quoted a report of "frequent" occurrence about Grand Rapids in the 1870's. Although much seemingly suitable habitat still occurs in the vicinity of all the old reported stations, the plant seems to have disappeared from its former haunts. No collections of snow trillium have been reported since 1939, when a plant was collected along Plaster Creek, Kent Co. Since no more recent collections were known and repeated searches failed to produce plants at the old stations, the Technical Advisory Committee to the Department of Natural Resources on Endangered Plants listed the trillium as probably extinct in Michigan (Wagner et al., 1977).

For most of the years of my interest in the Michigan flora, dating from about 1940, I have searched casually for the snow trillium. In 1960, G. Burrows and I prepared a paper on the genus *Trillium* in Michigan (Case & Burrows, 1962). We examined the major state herbaria and found no collections of *T. nivale* later than 1939, and few from any era. The status of *T. nivale* in Michigan, became, for us, a challenge. We asked ourselves: Did it grow in Michigan only as briefly established waifs from distant colonies in Indiana or Ohio? Or was this calciphile associated with gypsum soils and outcrops near Grand Rapids and tufa formations near Hubbardston? Or was the plant a very rare and local native overlooked because of its very early flowering season?

My wife, several of our botanically oriented friends, and I made the search for this plant a labor of love. We first scoured the old, documented localities as best they could be located, but to no avail! At Hubbardston, Ionia Co., we

walked miles of riverbank and climbed untold hills and bluffs but found no sign of the plant. We explored many habitats near Grand Rapids without success.

After many failures in Michigan, we sought out the plant in Indiana in order to gain a better understanding of its habitat. Our first observations were on limestone formations in the vicinity of Bedford and Oolitic where we found the plant to be local, but sometimes abundant. Subsequently, in central Indiana, we found the snow trillium in three somewhat different habitats: in crevices and on ledges of limestone outcrops, mostly near rivers and streams; on open, eroding soils free from grassy competition at the crests of wooded hillsides; and, occasionally, on gravelly floodplain soils in raw, open situations.

Armed with our Indiana experiences and with the knowledge that throughout its range *T. nivale* is strongly (but not exclusively) associated with specific river drainage systems, we concentrated our Michigan searches on the Grand River system (where it had occurred) and related drainage systems. In this area rock outcrops hardly occur; river bluff and floodplain habitats seem to be the only suitable habitats available. After nearly four decades of fruitless search, we began to believe that the plant truly no longer occurred in our state—but each spring we searched anyway.

I had long known that a brief post-glacial connection existed between the Grand and Saginaw River systems. Following the path of this former connection, certain bottomland or riverbank plants from a more southern flora (*Erythronium albidum*, *Jeffersonia diphylla*, *Fraxinus quadrangulata*, and *Quercus muhlenbergii*) have migrated from the Grand into the Saginaw River system. Since some of these plants are frequent companions of *T. nivale* elsewhere, it seemed possible that they might be associated with it here. We began, in 1978, a careful exploration of rivers and streams of the regions connecting these two river systems.

In May 1979, at a rock gardener's meeting at my home, James Briggs mentioned that he had in cultivation a tiny white trillium that his father-in-law, Candido Gonzales, had found on a streambank in Shiawassee County, in the Saginaw River drainage system. He was uncertain of the plant's identity. We were especially excited because the area was within a few miles of where we had ended our 1978 searches, and the habitat seemed to us especially similar to some of those we had seen in Indiana. At the conclusion of the meeting, I went with Mr. Briggs to his garden. The plant was *T. nivale* without question, but, of course, in fruit. He took me to its original station, and we found a colony of about 200 blooming-sized plants and quite a few seedlings. The plants grew on an elevated floodplain terrace which, while clearly floodplain, would be submerged only in an exceptionally heavy flood, perhaps no more than once in a dozen years. At this station there was some competition from grass, and the colony did not seem entirely secure.

In early April 1980, we scoured the habitat for considerable distances around this station. Access to woodlands and stream banks in this part of Michigan is very difficult as all such lands are private and most are posted. Most landowners cooperated, however, and we had success beyond our wildest dreams. We found six additional colonies of *T. nivale* within one to two miles of the original station. The amazing thing was the size of some of the colonies.

On the best sites, the plants numbered hundreds, indeed, thousands, as also reported by Steyermark (1963) for the few known colonies in Missouri. They almost always grew on sandy alluvium at the second floodplain level, above spring stream bed highwater level. As in the first situation, the plants grew on the level which would be under water only in exceptional seasons, years apart. The soil had an appearance of being "worked up"—bare, vaguely disturbed, occasionally humusy but not with a solid cover of leaf mold.

Forest cover varied considerably but consisted of blue beech (*Carpinus caroliniana*), american elm (*Ulmus americana*), silver maple (*Acer saccharinum*), box elder (*Acer negundo*), prickly ash (*Xanthoxylum americanum*), and chestnut oak (*Quercus muhlenbergii*). Almost always associated with the trillium were colonies of bladder nut (*Staphylea trifolia*). Violets, white and yellow adder's tongues, and hepaticas, both round and sharp-lobed, made up the main herb cover. Mostly, however, the snow trilliums kept somewhat apart, in open raw soil areas.

Peak bloom in 1980 was on April 9 (Fig. 1). At this time, the tiny plants, from three to six inches tall, sprawled slightly, but the flowers, large relative to the plant size, stood distinctly erect. The white or faintly pink petals were thinner-textured and more conspicuously veined in our plants than in central Indiana. The flowers had a strong, sweet, honey odor not unlike that of the bird's eye primrose (*Primula mistassinica*). Small honeybees or honeybee-like insects visited the blooms and fed voraciously. As the season progressed, the peduncles gradually recurved. Before the petals withered, the flower became less open and spreading and distinctly recurved. Finally, the peduncle declined below the leaves, and the whitish, three-angled fruit hung inconspicuously. The petioled, blue-green leaves withered very early in June, but long before the plant faded it was rendered nearly invisible by overgrowth of companion plants.

Protection of the large Shiawassee Co. colonies, in an area where the plant had not previously been known, will be pursued by the Nature Conservancy of Michigan. The fact that there are many plants in a few very localized colonies does not alter the fact that the plant is very rare and vulnerable in Michigan and urgently needs protection. Indeed, it was with considerable discomfort that I have brought this discovery to public attention since trilliums are particularly popular plants. I have deliberately tried not to be too specific on localities. But botanists do need to know of such discoveries, particularly when a species such as this has historical significance, has been considered extinct, and occurs considerably outside its general range.

After spending two weekends carefully locating and evaluating the Shiawassee County stations, we decided to see if our newly gained knowledge might aid in locating stations elsewhere. It was clear that in our early searches we had been too much influenced by our Indiana experiences with *T. nivale*. There it is mainly a plant of ledges and steep slopes with creeping soils. Here it seems to be exclusively a plant of floodplain alluvium. Continuing in our belief that the distribution of snow trillium related mainly to river drainages, we worked west along the tributary systems of the Maple and Grand Rivers into Clinton County. Here we found very little suitable habitat which was not too cut over or altered. Finally, in western Clinton County, we found a remnant of



FIG. 1. *Trillium nivale*, the Snow Trillium, in Shiawassee County, April 1980.

beech-sugar maple forest, a bit drier than the Shiawassee Co. habitat, which seemed to offer possibilities. Ground vegetation was much more abundant, both in numbers and species. Except for the presence on the floodplain of putty-root (*Aplectrum hyemale*) and white trillium (*T. grandiflorum*), the dominant species were as noted in Shiawassee County. Considerable exploration along the small creek banks at first yielded nothing, but in a humusy, plant-filled area at some distance from the creek we located about 100 snow trilliums. Imagine our excitement: 40 years of searching with no results, then hundreds of plants in two counties in just over two weeks time! Although further search failed to produce more stations, we are convinced that a careful exploration of the bottomlands of the Grand and other southern Michigan river systems will add localities for this plant.

Voucher specimens have been placed in the herbaria of the Cranbrook Institute of Science, University of Michigan, Michigan State University, and the U. S. National Herbarium. Figure 2 shows the known distribution in Michigan.

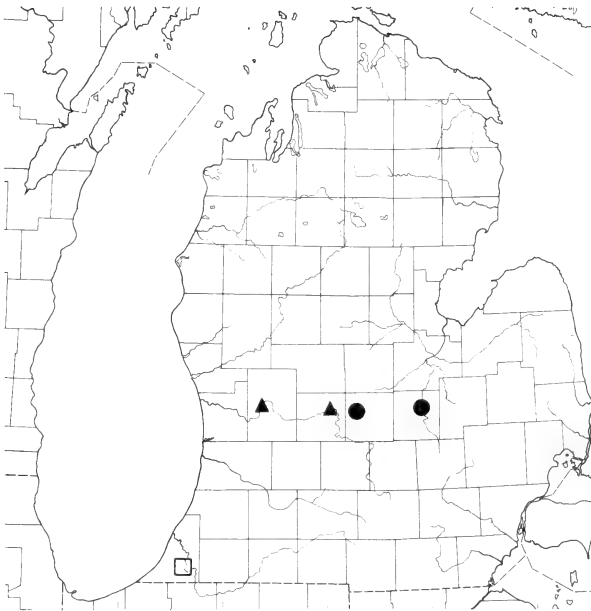


FIG. 2. Michigan distribution of *Trillium nivale*; triangles = recorded populations presumed to be extinct; solid circles = recent populations reported herein; open square = reported population (Beal, 1905) for which I have not seen a voucher.

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PUBLICATIONS OF INTEREST

RARE AND ENDANGERED PLANT SPECIES IN NEW ENGLAND. *Rhodora* Vol. 82, No. 829. January 1980. 237 pp. This special number of *Rhodora* includes 18 papers presented at a symposium in May of 1979 sponsored by the New England Botanical Club with support from the U. S. Fish and Wildlife Service. The papers include general ones on the biology of rare species and their protection as well as specific topics relating to New England states. The numerous persons and agencies in the Great Lakes region concerned with these timely matters will therefore find much of general interest as well as some data on the status of particular species. Copies of this substantial symposium proceedings are available at \$8.00 each from NEBC Symposium, Department of Botany and Plant Pathology, Nesmith Hall, University of New Hampshire, Durham, New Hampshire 03824 (checks payable to NEBC Symposium).

CLASSIFICATION OF WETLANDS AND DEEPWATER HABITATS OF THE UNITED STATES. By Lewis M. Cowardin, Virginia Carter, Francis C. Golet, & Edward T. LaRoe. U. S. Fish and Wildlife Service, Office of Biological Services FWS/OBS-79/31. 1980 ["1979"]. 103 pp. This new classification has been officially adopted by the Fish and Wildlife Service, which encourages other Federal and State agencies "to convert to the use of this system." So it will pay to be aware of it, even though many will find it difficult to refer to Scrub-Shrub Wetlands or Moss-Lichen Wetlands instead of bogs! Five basic systems are defined: Marine, Estuarine, Riverine, Lacustrine, and Palustrine. Classes based on substrate material and flooding regime, or on vegetative life form, may be the same under one or more of the systems. Dominance type, named for the dominant plant or animal forms, is the lowest level of the classification hierarchy.

NEW MOSS RECORDS FROM MANITOULIN ISLAND, ONTARIO

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As Ireland & Cain (1975) demonstrated in their checklist, our knowledge of the moss flora of Ontario is incomplete. They stated that differences in climatic, edaphic, biotic, and past geological factors are important in determining the moss flora. The interplay of these factors certainly has been responsible in shaping a unique vascular flora on Manitoulin Island (Morton, 1977). Crum (1966) was able to compile an unusually rich assemblage of disjuncts from northern areas and the Rocky Mountains in the area of Owen Sound and the Bruce Peninsula. Manitoulin Island, lying near the tip of the Bruce Peninsula, shares many similar physiographic characteristics. Thus, Manitoulin Island should be expected to contain an equally rich and diverse moss flora.

To date, there has been no comprehensive inventory of the mosses of Manitoulin Island. Ireland & Cain (1975) recorded 138 species for the District of Manitoulin, many of which are based on single collections. During 1979, in casual collecting, I found 48 species from Greenbush Swamp, on the north-eastern corner of Manitoulin Island. Although the list is by no means complete, I would like to report nine new records.

Greenbush Swamp, is located 7 km. southwest of the Town of Little Current, on the 5th Concession of Howland Township. The swamp is predominantly white cedar (*Thuja occidentalis*), with young stands of black ash (*Fraxinus nigra*) along the wetter periphery. There are two seasonally flooded pockets of silver maple (*Acer saccharinum*) in the southern half of the swamp. The northeastern corner is largely a wetland sedge and shrub community. Steep limestone cliffs define the basin with young deciduous forests immediately surrounding the swamp. All species collected from Greenbush Swamp are commonly found in such habitats in the Great Lakes Region.

Voucher specimens have been deposited in CANM and in the author's personal collection.

Sphagnum nemoreum Scop.
Plagiomnium ellipticum (Brid.) Kop.
Rhizomnium appalachianum Kop.
Campylium polygamum (B.S.G.) C. Jens.
Leptodictyum riparium (Hedw.) Warnst.

Brachythecium oxycladon (Brid.) Jaeg. & Sauerb.
Plagiothecium denticulatum (Hedw.) BSG
Hypnum pratense Koch ex Brid.
Orthotrichum sordidum Sull. & Lesq. ex Aust.

I would like to thank Dr. R. R. Ireland for aid in identification. The assistance of Dr. R. J. Hebda both in the field and in the laboratory is appreciated. Drs. Ireland and Hebda provided comments on the manuscript.

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REVIEW

MICHIGAN TREES. Revised and Enlarged Edition of Charles Herbert Otis's *Michigan Trees*. By Burton V. Barnes and Warren H. Wagner, Jr. University of Michigan Press, Ann Arbor, 1981. 384 pp. \$5.95 (paper); \$10.95 (cloth).

Fifty years after the previous revision of "Otis," which remained a best-seller for the University of Michigan Press, this long-anticipated and thorough updating appeared in time for the 1981 field season. Unfortunately, Otis himself (U. of M. B.S. '10, Ph.D. '13) died in Ohio at the age of 93 on July 25, 1979, two years too soon to see this handsome successor to his work. With a few improvements, the illustrations are essentially the same as in the old "Otis"; key characters are added in a list beneath each. Otherwise, the book is quite new. There is an excellent introductory section of 50 pages with concise and modern treatments of the characters of trees and the habitats and communities of Michigan, with many helpful maps and drawings. New keys to genera in summer and winter are, as in the old editions, followed by treatments of the genera by families, with further keys to species and details on morphological characters, distribution, and habitat. The basic arrangement of groups follows the Cronquist system for the flowering plants.

The text has been thoroughly rewritten out of the extensive experience of the authors, both active field botanists as well as researchers on woody plants. The result is an up-to-date treatise which is both authoritative and useful, and deserves to continue the widespread popularity of "Otis" in Michigan and neighboring regions. There is a new supplementary section on selected shrubs and woody vines, which is likely to be frustrating because it is intentionally very incomplete. However, almost all native tree species (except for *Crataegus*) are included, although a few rare ones, such as swamp cottonwood and rock chestnut oak, as well as the more common showy mountain-ash, are only mentioned, with distinguishing characters, under similar species. Many hybrids are cited; data are provided for the largest Michigan specimen of each tree; there is a glossary and a helpful list of references. About the only feature of the old "Otis" omitted from this edition is the section on woods.

-E. G. Voss

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On the cover: *Red Cedar (Juniperus virginiana)*—*Cottonwood (Populus deltoides)* savanna, Long Point, Norfolk County, Ontario.
Photo by P. M. Catling, 21 Sept. 1979.

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THE

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March, 1982



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Articles dealing with any phase of botany relating to the Upper Great Lakes Region may be sent to the editor in chief. In preparing manuscripts, authors are requested to follow our style and the suggestions in "Information for Authors" (Vol. 15, p. 238).

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THE DISTRIBUTION OF *SOLIDAGO OHIOENSIS*¹ [7]

James S. Pringle

Royal Botanical Gardens, Hamilton, Ontario

Solidago ohioensis Riddell, the Ohio Goldenrod (Fig. 1), is almost totally restricted to the Great Lakes region. Details of its distribution are of interest because of its limited range and because it exemplifies especially well a distribution pattern shared with a number of other rare and local species in this region.

Distribution records for *S. ohioensis* mapped in Fig. 2 are based on specimens examined in ALTA, ASU, BGSU, BH, BHO, BU, BUF, CAN, CM, CU, DUKE, E, F, GH, HAM, HNH, ILL, IND, K, KE, MICH, MIN, MO, MOR, MSC, MU, NCU, NHA, NO, NY, NYS, OAS, OS, QK, SLU, TENN, TEX, TRT, TRTE, UBC, UMBS, UWO, VT, WLU, WMU, WTU, WVA, and the herbaria of the Franz Theodore Stone Laboratory and the Simcoe County [Ontario] Museum. Records previously mapped by Salamun (1964), based on specimens that included those in MIL, UWM, and WIS, have also been accepted. No specimens of *S. ohioensis* were found in APSC, DEN, KNK, MUS, or WIN.²

The range of *S. ohioensis* is divided into a southern part, from southern Ohio and central Illinois north to the shores of Lake Erie and southern Lake Michigan, and a northern part along the northern shores of Lakes Huron and Michigan (Fig. 2). The disjunction in its range, noted in Wisconsin by Salamun (1964), extends across Michigan and into Ontario. It seems unlikely that this gap in records is due to the destruction of all populations of *S. ohioensis* in these areas before any collections were made, in view of its persistence elsewhere, even in urban areas. Field studies of *S. ohioensis* indicate, instead, that this gap reflects a natural absence of suitable habitats.

In the southern part of its range, many populations of *S. ohioensis* are in wet, tall-grass prairies. In Wisconsin, Curtis (1959) found these to be the communities in which this species most frequently occurs. Dominant grasses with which *S. ohioensis* is commonly associated in wet prairies include *Calamagrostis canadensis* (Michx.) Beauv., *Spartina pectinata* Link, and *Andropogon gerardii* Vitman. Among the more abundant forbs are *Thalictrum dasycarpum* Fisch. & Lall., *Zizia aurea* (L.) W. D. J. Koch, *Pycnanthemum virginianum* (L.) Durand & Jackson, and *Aster firmus* Nees.

As noted by Wood (1836) and Curtis (1959), the soil surface of wet prairies is usually uneven, with hummocks 15–30 cm higher than the surrounding land being better drained and escaping periodic flooding. In such conditions, *S. ohioensis* is usually found near or in the bottoms of the depressions. The drier portions of a wet prairie may lack *S. ohioensis* altogether, as Hayes (1964) has shown in his studies of the prairies in the St. Clair delta.

¹Contribution from the Royal Botanical Gardens, Hamilton, Ontario, No. 34, and from the University of Michigan Biological Station.

²Standard herbarium abbreviations follow Holmgren & Keuken (1974).



Fig. 1. *Solidago ohioensis* at Long Point, Haldimand-Norfolk Region, Ontario.

Solidago ohioensis also occurs in fens (as defined by Curtis, 1959, Pringle, 1980, and Stuckey & Denny, in press) in the southern part of its range. Betz (1965) considered it to be one of the most useful indicator species of alkaline fens in the Chicago area. As Curtis (1959) noted, fens in the Great Lakes region have much in common ecologically and floristically with wet prairies. In both of these habitats, *S. ohioensis* may be associated with such dominant species as *Spartina pectinata*, *Calamagrostis canadensis*, *Sorghastrum nutans* (L.) Nash, and *Thalictrum dasycarpum*.

Stuckey & Denny (in press) divided the fens of Ohio into "bog fens" and "prairie fens." Bog fens contain a number of species that range primarily to the east and north, some of these also occurring in acid bogs; prairie fens contain a higher proportion of species that are also characteristic of wet prairies. *Solidago ohioensis* was found by them to occur regularly in both kinds of fens.

Moist depressions, known as pannes, wet sand-flats, or slacks, among the dunes along the shores of the Great Lakes are the habitat of *S. ohioensis* in the northern part of its range. These pannes are notable as the chief or only habitats of many rare, disjunct, and endemic species. As "high-moor formations,"³ the pannes of the Bruce Peninsula, Ontario, were described by Klugh (1912). Similar but older and more stable communities at the southern end of Lake Michigan were described by Gates (1912).⁴ Pannes in the northern part of the Great Lakes region share relatively few dominant species with wet prairies and fens, although *Calamagrostis canadensis* and *Schizachyrium scoparium* (Michx.) Nash may be abundant in all three. More characteristic panne dominants, in the zone occupied by *S. ohioensis*, include *Cladium mariscoides* (Muhl.) Torr., *Carex interior* Bailey, *C. sterilis* Willd., *Juncus balticus* Willd., *J. brachycephalus* (Engelm.) Buchenau, *Myrica gale* L., and *Potentilla fruticosa* L. *Cladium mariscoides* and *Potentilla fruticosa* are also frequent and sometimes among the dominants in fens. Other common associates of *S. ohioensis* in both fens and pannes include *Parnassia glauca* Raf. and *Agalinis paupercula* (A. Gray) Britton.

Wet prairies, fens, and pannes are all communities in which herbaceous plants receive abundant light, there being few trees or large shrubs; all have a plentiful and steady water supply; and their soils are calcareous, ranging from near-neutral to moderately alkaline, with a high content of relatively coarse organic and/or mineral matter.

None of the three habitats of *S. ohioensis* is extensive in the Great Lakes region. As mapped by Transeau (1935), prairies constituted 10 per cent or more of the original vegetation only within the areas outlined in Fig. 2, and were almost totally absent north of 43° N and east of 82° W. Within the general limits of prairies, moreover, wet prairies are further restricted. Wood (1836) and Sears (1926) observed that, in Ohio, wet prairies occur almost exclusively in the glaciated northern and west-central parts of the state; the prairies farther south are

³"High-moor formations" was unfortunately applied to panne communities by Klugh, because this term is ordinarily applied to acid, ombrotrophic raised bogs. *Solidago ohioensis* was misidentified as *S. riddellii* Frank by Klugh.

⁴In the older and more southerly complexes studied by Gates, however, wet-prairie communities, dominated by *Andropogon gerardii*, *Sorghastrum nutans*, *Liatris spicata* (L.) Willd., and *Solidago ohioensis*, had developed on the stabilized interdunal-panne sites.

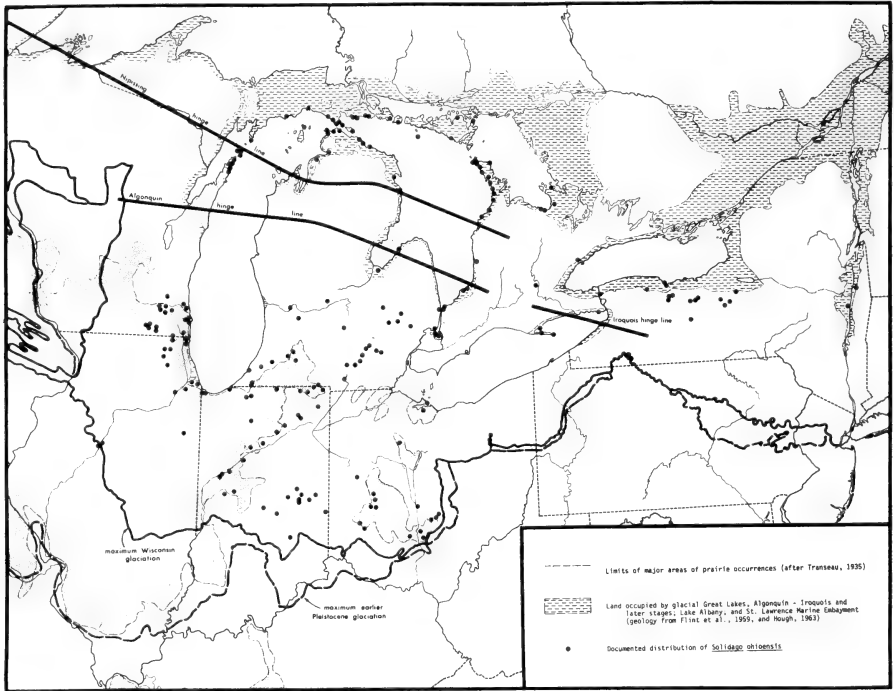


Fig. 2. Documented distribution of *Solidago ohioensis*.

mostly dry prairies or "barrens" (Wood, 1836; Braun, 1928). Deam (1925) and Gordon (1936) indicated that wet prairies occur mostly in the northern part of eastern Indiana and in the northern and central parts of western Indiana. The relationship between glaciation and the presence of wet prairies in Illinois was noted by Sampson (1921). Curtis (1959) reported wet prairies only in southeastern Wisconsin.

Fens are strictly associated with glaciated topography south of the Great Lakes. Although extensive wetland areas in the boreal forest are often classified as fens, Curtis's (1959) studies indicated that fens conforming to his narrower definition, i.e., of the type occupied by *S. ohioensis*, are rare in the northern part of the Great Lakes region, where comparable topographic situations are generally associated with more acid soils having less mineral content. Fens are, moreover, more commonly associated with moraines than with till plains (Pringle, 1980; Stuckey & Denny, in press). Populations of *S. ohioensis* extending from north-central Indiana to southeastern Michigan, for example, are conspicuously aligned with the Packerton and adjacent Mississinewa moraines, and a cluster of populations in east-central Indiana is associated with the Farmersville moraine. East of the Appalachian escarpment, fens are rare because of the limited extent of calcareous substrates.

Geologic factors related to the occurrence of interdunal pannes in the Great Lakes region are indicated in Fig. 2. North of the hinge lines, extensive

portions of the beds of earlier lake stages have been, and continue to be, gradually exposed, as a result of the differential uplift of the earth's crust following deglaciation, and the downcutting of the St. Clair outlet (Hough, 1963; Zoltai, 1969; Dorr & Eschman, 1970). In some areas, these emerging lake beds rise very gradually from the present shores, which are paralleled for much of their length by a series of low dunes that indicate former shoreline positions. Because of the gradual slope, the depressions among the more recently formed dunes are close to lake level and are therefore constantly moist. South of the hinge lines, moist interdunal depressions are rare except in a few areas of extensive deltaic deposits (cf. Fig. 2 and Dorr & Eschman's [1970] map of "areas of modern sand movement and foredune growth" in Michigan).

Thus the southern portion of the range of *S. ohioensis* appears to be limited on the south, east, and north by the extent of wet, tall-grass prairies and calcareous, grass-dominated fens. The gap in its range occurs between the northern limits of these communities and the southern limits of interdunal pannes. Its western limits are probably determined in some areas by the availability of wet-prairie and fen habitats, but appear to be related primarily to the Wisconsinan survival area of this species and to its postglacial migration.

As noted by Voss (1954), *S. ohioensis* is absent outside the limits of Wisconsinan glaciation. Nevertheless, it seems unlikely that *S. ohioensis* is of post-Wisconsinan origin. This species is diploid ($2n = 18$; Kapoor & Beaudry, 1966, SE Wisc.; Pringle, 1979, N Lower Mich.), and in much of its range it frequently grows with those diploid species to which it is most closely related. A few hybrids are known (Salamun, 1964; Bernard, 1969; records in CU, F, and MICH), but there is no true intergradation between *S. ohioensis* and any other species.

Assuming that *S. ohioensis* is of pre-Wisconsinan age, it seems most likely that it survived the Wisconsinan period south of the glacial front in and near southeastern and south-central Ohio. Although there are no records of *S. ohioensis* from this unglaciated territory, the greatest concentration of records near the glacial maximum is immediately to the north of this region. The unglaciated portions of Ohio and adjacent states apparently now provide no suitable habitats for *S. ohioensis*, but fenlike conditions may have been present during the glacial period. Thus the range of *S. ohioensis* may have been greatly restricted during the glacial maximum, and postglacial changes in climate and drainage may have eliminated the habitats in which it survived. Following deglaciation, however, the development of fens and wet prairies would have permitted the rapid spread of *S. ohioensis* in the glaciated portions of Ohio, southern Michigan, and northeastern Indiana. Subsequently, the development of dune-swale complexes in the deltaic deposits near the southern end of Lake Michigan would have provided a migration corridor extending to southeastern Wisconsin. The absence of *S. ohioensis* from the wet prairies and fens of Iowa and Minnesota and its limited occurrence in Illinois indicate that, unlike many prairie species, it did not spread into the Prairie Peninsula (term from Transeau, 1935) from a glacial survivorium farther west or southwest. Its postulated migrational history is, however, compatible with observations by Gleason (1932) and Curtis (1959) that many species in the wet prairies of the Prairie Peninsula, including some of the dominant species with which *S. ohioensis* is most often

associated, constitute an "Allegheny meadow element" (term from Curtis, 1959), which evidently migrated into this region from the southeast, and that a significant proportion of such species in the wet prairies are absent from Iowa and Minnesota (Curtis, 1959).

A number of other species growing in pannes and fens and/or wet prairies have distribution patterns more or less similar to that of *S. ohioensis* in the Great Lakes region, although in most cases their total ranges are more extensive. Special note may be made of *Scleria verticillata* Willd., *Zigadenus glaucus* (Nutt.) Nutt., and *Tofieldia glutinosa* (Michx.) Pers., because Voss's (1972) maps of their distribution in Michigan show that these species are widespread in the southern part of the state but occur only near the shores of the Great Lakes farther north, with similar disjunctions between the southern and northern parts of their ranges. Other examples include *Parnassia glauca* Raf., *Lobelia kalmii* L., *Cacalia tuberosa* Nutt., and *Prenanthes racemosa* Michx. *Zigadenus glaucus* and *L. kalmii* (total ranges mapped by Foos, 1971) can also be cited as species that are relatively widespread in Ohio but similarly restricted to the northern part of Illinois.

I am grateful to the curators and staff of the herbaria listed for opportunities to examine specimens and to Dr. Ronald L. Stuckey for comments on the manuscript at various stages in its development.

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MICHIGAN PLANTS IN PRINT

New Literature Relating to Michigan Botany

This section lists new literature relating to Michigan botany under four categories: A. Maps, Soils, Geology, Climate (new maps and selected bulletins or articles on matters useful to field naturalists and students of plant distribution); B. Books, Bulletins, etc., and C. Journal Articles (listing, respectively, all separate publications and articles in other periodicals which cite Michigan specimens or include research based on plants of wild origin in Michigan—not generally including work on cultivated plants nor strictly economic aspects of forestry, conservation, or agriculture); D. History, Biography, Exploration (institutions as well as travels and lives of persons with Michigan botanical connections). When the subject matter or relation to Michigan is not clear from the title, annotations are added in brackets. Readers are urged to call to the editor's attention any titles (1960 or later) which appear to have been overlooked—especially in less well known sources.

—E. G. V.

A. MAPS, SOILS, GEOLOGY, CLIMATE, GENERAL

- Austin, Franklin R. 1979. Soil Survey of Kalamazoo County, Michigan. U. S. Dep. Agr. 102 pp. + 72 folded map sheets + [5] folded sheets. [The map sheets include complete aerial photographic coverage at a scale of about 4 inches to the mile, with boundaries of soil types superimposed. A welcome replacement for the old survey of the county made in 1922 and published in 1926. The other 9 soil surveys listed below are similar in format, and all are available from the Michigan Agricultural Experiment Station, M. S. U.; the Soil Conservation Service, 1405 South Harrison Rd. Room 101, East Lansing 48823; or from the appropriate local offices of the Soil Conservation Service and Cooperative Extension Service.]

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No one expects that tearing up a woods to build a tractor road will yield exciting bryophytes, and certainly not in the Keweenaw Peninsula where bryologists have long sought for western disjuncts and northern refugees. Nevertheless, when a woodland tract by the freshman parking lot at Michigan Technological University in Houghton experienced such an upheaval in August and September of 1978, the soil was invaded by opportunistic mosses, including several that had been overlooked in the area. The road was used only a short time and had already been undisturbed for 33 months when this reconnaissance began. By the summer of 1981, 11 species of mosses were established on the west side of the road, along a shallow ditch in light shade from the edge of the woods.

The most obvious moss, covering sides and crests of tractor tread depressions, was *Trichodon cylindricus* (Hedw.) Schimp. (Glime 5557), a western species, rare in the East, previously recorded from Mt. Bohemia, Keweenaw Co. (Crum, 1976), as well as Labrador, Newfoundland, and New Brunswick (Ireland, 1978). Producing abundant capsules during the study period (15 May–6 July), it covered the edges of the roadcut for nearly 50 meters, providing 20–50% cover. The soil was frequently black because of blue-green algae (*Scytonema*, *Oscillatoria*, and *Nostoc*).

Mixed with *Trichodon* in scattered 1–2 cm patches were several other previously overlooked species: On 27 May, *Physcomitrium pyriforme* (Hedw.) Hampe was abundantly fruiting, but it disappeared by 6 July. This is a first report for the Upper Peninsula (Glime 5584). *Trematodon ambiguus* (Hedw.) Hornsch., a species of disturbed soil, discovered in Keweenaw (Glime 5141) and Houghton Co. (Glime 5105) last year, was fruiting on 5 July in this area. *Barbula unguiculata* Hedw. was previously reported for the Upper Peninsula only from Mackinac Co. (Darlington, 1965).

Other bryophytes scattered among the *Trichodon* and such field flowers as *Chrysanthemum* and *Trifolium* were typical of disturbed soil (*Barbula convoluta*, *Bryum argenteum* and two other species of *Bryum*, *Funaria hygrometrica*, and *Leptobryum pyriforme*) or invaders from the adjoining forest (*Atrichum undulatum* and *Thuidium delicatulum*).

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FLY-MEDIATED SPORE DISPERSAL IN
SPLACHNUM AMPULLACEUM (MUSCI).

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Splachnum ampullaceum is a member of a family unique among the mosses because of specialized substrate requirements and mode of spore dispersal (Bequaert, 1921, Erlanson, 1935). Steere (1958) listed the odd habitat specialization and capsule structure in this family, the Splachnaceae, as representing one of four distinct evolutionary lines in mosses. Numerous taxa in the family are restricted to the dung of mammals, organically enriched soils, or other organic debris, such as skeletal remains or regurgitated stomach pellets of owls. The spores of a number of taxa are apparently transported by flies. *S. ampullaceum* is normally limited to cold temperate latitudes. It has been collected in British Columbia and Alberta and from Ontario and Michigan eastward to Newfoundland, Massachusetts, and New York, and as far southward as West Virginia. It has been reported from central Europe, Siberia, and Japan (Crum et al., 1972). The growth habit consists of tightly clumped leafy gametophores which conform to the shape of the substrate (deer dung, cow dung, etc.). The leafy plants range from one to four cm tall, and the setae may attain a height of 6.5 cm (Crum, 1976). When the apophyses (enlarged necks of the capsules) are fully expanded, they often make contact with adjacent apophyses resulting in a dissected topological surface consisting of the upper surface of the apophyses and the plane of space connecting them. The numerous apophyses form brightly colored islands on this surface (Fig. 1).

Bryhn (1897) first observed dipterans visiting the sporophytes of *S. rubrum* Hedw. Few reports have appeared in the literature describing the interactions between the plants and insects since Bryhn's observations. Insects which have been identified as possible spore dispersal vectors include *Phorbia* sp. (Bequaert, 1921) and *Lucilia caesar* (Wettstein, 1921) for *Tetraplodon mnioides* and muscids, dung flies, and blow flies for *S. rubrum* (Bryhn, 1897). Muscidae are reported to be attracted to capsules of *S. vasculosum* and a mixture of *S. ampullaceum* and *S. luteum* (Koponen & Koponen, 1977). Wettstein (1921) reported observing *Scatophaga cineraria* Meig. and *Copromyza nitida* (Meig.) visiting *S. sphaericum*. Only Bryhn (1897) reported actually seeing the flies visit fresh substrata after leaving the sporophytes.

Conflicting reports are present regarding the nature of the plant-insect interaction. Bequaert (1921) reported flies licking a sticky substance from the upper surface of the apophysis of *Tetraplodon mnioides*. This he stated was probably secreted through numerous stomata. On the other hand, Crum (1972)

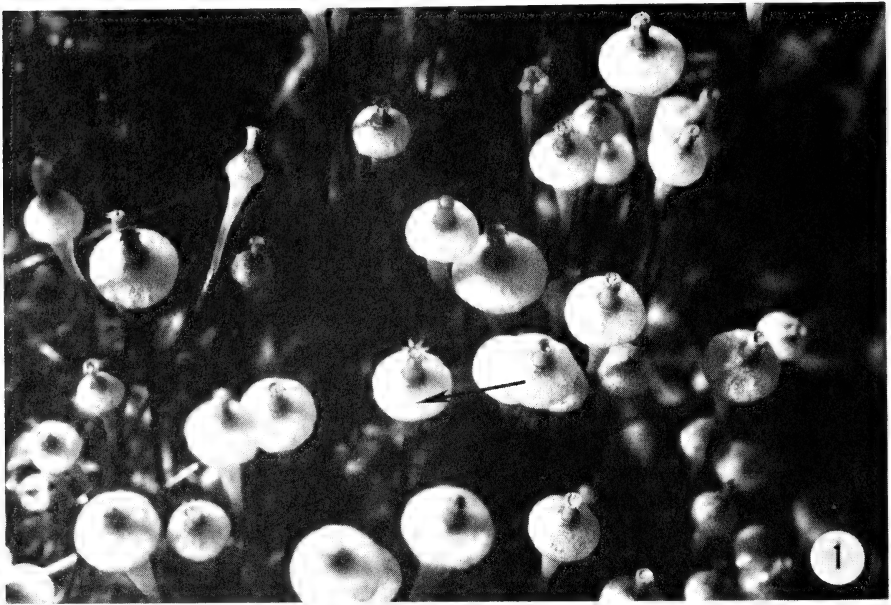


Fig. 1. Sporophytes of *S. ampullaceum*; arrow points to enlarged apophysis, X5.

called the flies “dupes of nature” since they may be doing work for the plant (spore dispersal) while gaining no benefit for themselves. In this sense the flies may be compared to those that visit carrion blossoms of the angiosperm genus *Stapelia* (Faegri & van der Pijl, 1979). Similarly, sporophytes of *S. ampullaceum* produce chemical cues which induce a behavioral pattern in a specific insect and result in that insect visiting the plants. The inadvertent transport of spores to fresh substrata may be a result of this interaction.

The purpose of our study was to document the activities of insects visiting *S. ampullaceum* in its natural habitat. We captured and identified insect visitors, noted their behavior while on the sporophytes (as well as their approach and departure), and documented the frequency of spore transport (i.e., the number of flies with spores on their bodies) and the distribution of spores on the flies.

A small population was located in a black spruce (*Picea mariana*) bog along the northwest shore of Stutsmanville Lake, Emmet Co., Michigan (T35N, R6W, Sec 24), growing on what appeared to be humified deer dung. The population consisted of approximately 100 sporophytes in a single patch at the base of a small clump of black spruce.

Dipterans visiting the plants were netted and killed with ethyl acetate. A total of 15½ hours was spent in collecting flies and another seven hours in observing the flies. A number of flies were marked with ‘Aurora Pink’ fluorescent powder in order to follow the movement of individuals. Captured flies were identified by Cecil Smith of the Entomological Museum at the University of Georgia. Voucher specimens of the plant and insects are in the University of Georgia Herbarium (GA) and Entomological Museum.

Preparations for SEM consisted of mounting *Pyrellia cyanicolor* on a stub with double sticky tape and coating with gold/palladium for six minutes in a Technics, Hummer 5, sputter coater. Micrographs were made with a JEOL-JSM 35 SEM.

Six taxa of dipterans were captured on the sporophytes (Table 1). A total of 71 flies was collected. Spores were observed on only four flies, all of the genus *Pyrellia*. Spores were located on the tarsus, femur and tibia of forelegs and on the trochanter and femur of midlegs (Fig. 2) attached to the cuticle or hairs (Fig. 3). They may have been attached to the insect by an amorphous, sticky substance (Fig. 4) hypothesized by Bequaert (1921) and Crum (1976).

Two types of approach to the plants by members of the Muscidae were observed. The majority of the flies landed first on surrounding vegetation, fallen logs, or black spruce roots in close proximity to the sporophytes and then oriented themselves toward the sporophytes and moved onto them. Alternatively, flies landed directly on the apophysis. Members of the Sepsidae were observed around or on the plants almost continually during favorable weather. Although they contacted the spore-bearing regions of the plants, none of those captured had spores attached to their bodies.

The muscids moved easily over the tops of the apophyses, going from capsule to capsule, often using their forelimbs to grab an adjacent sporophyte, pull it closer, and then move to it. An individual fly often contacted a number of capsules in this way. Flies also walked among the setae, beneath the apophyses, and occasionally on the gametophores. The length of a visit for the muscids ranged from a second or two to longer than a minute (Troilo & Cameron, 1981). Flies were also observed departing and then returning to the plants.

Other behaviors observed while the flies were on the plants included proboscis extension and grooming. Proboscis behavior consisted of 1–3 brief

TABLE 1. Dipterans captured on the sporophytes of *Splachnum ampullaceum*. (Less than half of the flies observed on the sporophytes were actually collected.)

	Number collected	Number with spores
MUSCIDAE		
<i>Pyrellia cyanicolor</i> Zett.	37*	4
<i>Myospila metitabunda</i> (Fab.)	14*	0
Undetermined	1	0
CEPSIDAE		
<i>Cepis</i> sp.	14*	0
CALLIPHORIDAE		
<i>Lucilia illustris</i> (Meig.)	3	0
SYRPHIDAE		
Undetermined	1	0
ANTHOMYIIDAE		
<i>Anthomyiinae</i> sp.	<u>1</u>	<u>0</u>
TOTAL	71	4

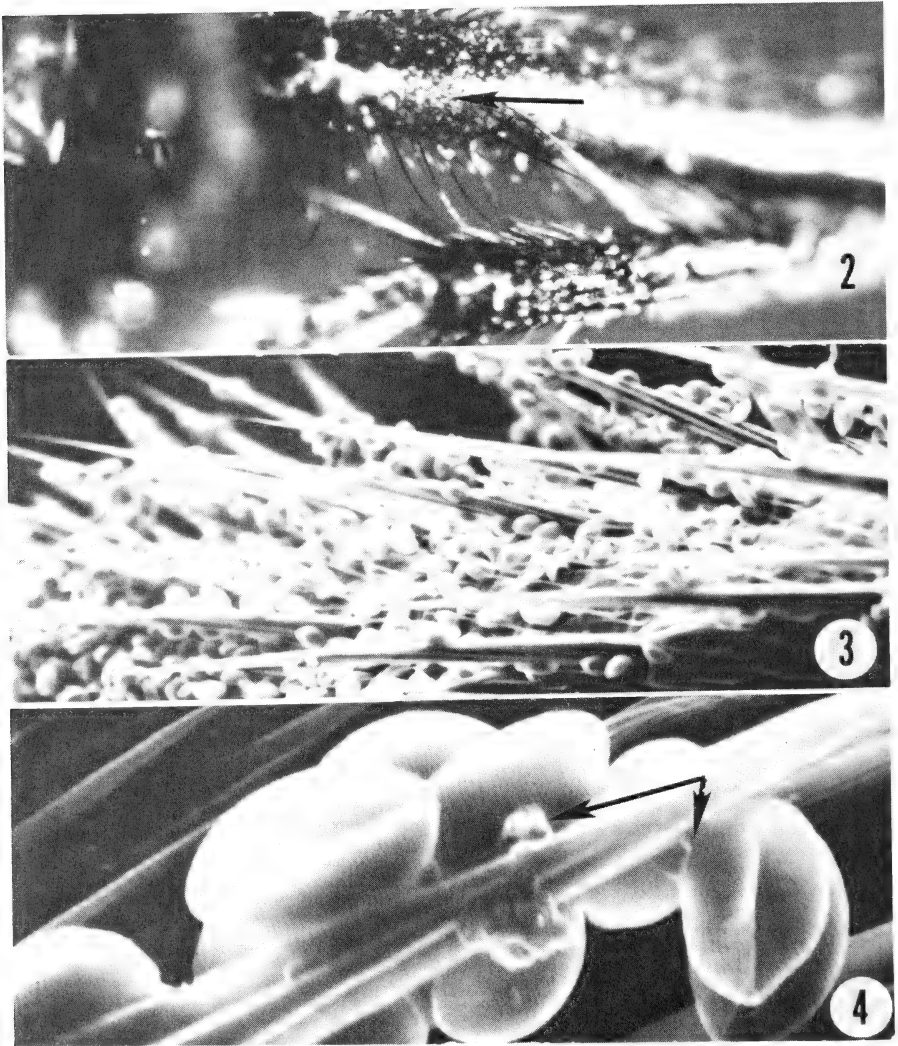


Fig. 2. Light micrograph of spores (arrow) of *Splachnum ampullaceum* on the tarsus and femur of the foreleg of *Pyrellia cyanicolor*, $\times 725$.

Fig. 3. SEM of spores of *Splachnum ampullaceum* on the femur of the foreleg of *Pyrellia cyanicolor*, $\times 425$.

Fig. 4. SEM of spores attached to hairs of the tarsus of the foreleg of *Pyrellia*. Note amorphous material between the spores and their point of attachment to the insect (arrow), $\times 3500$.

extensions in which contact was made with the upper surface of an apophysis. However, this contact was of the shortest possible duration, the proboscis being withdrawn upon contact with the apophysis. Grooming the head with the forelimbs was observed while flies were on the sporophytes and after they left the plants and were resting on surrounding vegetation.

The results of this study and that of Troilo & Cameron (1981) indicate that dipterans are actively attracted to *Splachnum ampullaceum*. Attraction consists of two components, as hypothesized by Bequaert (1921). Long-distance attraction is by volatile compounds produced by the plants, and short-distance attraction is by brightly pigmented apophyses and compact growth habit. Evidence for the importance of color and the macroscopic form of the tightly clumped sporophytes comes from previous studies on the color vision of *Phormia regina* and *Calliphora* sp. (Moring, 1978) and *Musca domestica* by Fukushi (1976) and our observations made during senescence of sporophytes. During this period the majority of sporophytes were lying horizontally. A slight odor (to human olfaction) was still present. Flies continued to frequent the immediate area of the plants, but only rarely did they move to the moss in contrast to a high frequency of visits when the setae were upright. In addition to the change in the position of sporophytes, the apophyses underwent a color change. When the capsule was mature, the apophysis was bright-yellow with small patches of wine-red color, and the surface appeared to be covered with a glossy coating which glistened in the light. Upon aging the apophyses became progressively more reddish and shrunken. At the same time that the setae no longer held the capsules upright, the apophyses turned reddish-purple and were reduced to less than half their fully expanded size. This color change was probably at least partially responsible for the lack of flies on the moss during this period.

Other observations indicate that temporal partitioning of insect-spore dispersal vectors may occur. The vast majority of visits by the genus *Pyrellia* occurred on clear days with temperatures of 25-30°C. On days when the temperature was less than 25° and the skies were overcast, mostly members of the genus *Myospila* were observed visiting the plants. This could account for the lack of spores on these flies, since during cool, humid weather the peristomes do not recurve, thereby keeping the spores protected inside the capsules. According to Cole (1969), *Pyrellia cyanicolor* (the only North American species) ranges across North America; however, its biology is virtually unknown. Cole reported only that the larvae breed principally in cow dung, as do *Myospila* larvae, and that both are general scavengers.

Janzen (1980) defined coevolution as change in a trait of the individuals in one population in response to a trait of the individuals of a second population, followed by an evolutionary response by the second population to the change in the first. Therefore, the possibility of coevolution between *S. ampullaceum* and its insect visitors, in the sense of many angiosperms and their pollinators (Macior, 1971), does not appear likely, at least in this system. While it does appear evident that *S. ampullaceum* has evolved in response to the dipterans it attracts, there is no evidence that the dipterans have evolved in response to the plants. The forces which would bring about a change in the genotypic frequency of the flies, i.e., those that increase the fitness of the visitor (food, protection

from predators, etc.) have not been observed in this system. The brief contact of the apophysis with the proboscis of the fly is not indicative of feeding behavior (Dethier, 1976; Troilo & Cameron, 1981). However, although it does not seem likely, we cannot rule out the possibility of spores being eaten by flies, as reported for members of the gasteromycete family Phallaceae (Ingold, 1971). Nor can we rule out the possibility of the flies being rewarded by increased surface temperatures of the apophyses, resulting in increased metabolic rates of insects which landed on them, and thereby possibly increasing their foraging abilities or fecundity during periods of suboptimal weather (Hocking & Sharplin, 1965). This also seems unlikely, however, as visits of *Pyrellia*, the only flies that actually transported spores, occurred during relatively warm, sunny weather.

The small number of flies with spores on their bodies suggests inefficient spore dispersal. However, this study did not include observations of the early period of spore presentation. Steere (personal communication) has noted that spores of *S. rubrum* are presented as a large mass during the early days of maturity. If this is also true in *S. ampullaceum*, the majority of spores may have been dispersed before our study was initiated. Other reasons for finding so few flies with attached spores include grooming (which may have resulted in the removal of spores) and netting of flies soon after they landed on the sporophytes (which reduced the time spent on the plants and the number of sporophytes visited). The presence of a high degree of morphological and physiological specialization in *Splachnum ampullaceum* indicates that it is, apparently, very finely tuned to the dipterans it attracts. The complexity of this relationship may be compared to that found in highly advanced angiosperms. The dispersal of spores by flies to habitats suitable for germination and continued development with a relatively high probability of success could have many genetic consequences. One of these may be a lower inbreeding coefficient. A single fly visiting a number of individual populations (clumps) consecutively, inadvertently gathering spores at each site, may upon visiting a rewarding substrate (to both plant and animal) disperse spores from a number of populations to that single location. This possibility could be tested experimentally by comparing the inbreeding coefficient of this and similar taxa to taxa with wind-dispersed spores or other mechanisms of spore dispersal found in plants dependent on free water for fertilization and possessing a dominant haploid generation. An energy savings, in terms of lower numbers of spores produced, may also occur as a result of entomophily.

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REVIEW

THE ARCTIC-ALPINE ELEMENT OF THE VASCULAR FLORA AT LAKE SUPERIOR.

National Museums of Canada, Publications in Botany No. 10. By David R. Given and James H. Soper. 1981. 70 pp.

Here, copiously illustrated with habitat photographs and detailed distribution maps for representative species, is a long-awaited account of those more or less disjunct boreal taxa that make such places as Isle Royale and the Keweenaw Peninsula, as well as the Ontario shore of Lake Superior, fascinating to the plant geographer. Of the 48 taxa selected as constituting the arctic-alpine element at Lake Superior, 31 occur in Michigan, and of these, 22 are currently listed as "threatened" in the state. This little volume will help to place them in phytogeographic and ecological perspective.

—E. G. Voss

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TOMENTHYPNUM FALCIFOLIUM IN MINNESOTA ✓

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During the summer of 1977, in Itasca County, northern Minnesota, a moss was collected that was considered to be *Tomenthypnum nitens* (Hedw.) Loeske. On more careful examination, however, falcate-secund leaves revealed the plant to be *T. falcifolium* (Ren. ex Nich.) Tuom. Whereas *T. nitens* is known from scattered stations in central and northern Minnesota (Beltrami, Clearwater, Hennepin, Hubbard, Itasca, Koochiching, and Stearns Cos.), this is the first known station for *T. falcifolium* in the state. As pointed out by Vitt & Hamilton (1975) *Tomenthypnum nitens* is a species of rich fens, whereas *T. falcifolium* seems to prefer more acid conditions, such as near the tops of hummocks. In Itasca County *T. falcifolium* was collected from the side of a *Sphagnum*-dominated hummock in a rather open place in a swamp dominated by *Picea mariana* and *Larix laricina*, with occasional *Thuja occidentalis*. Vascular plants nearby included *Chamaedaphne calyculata*, *Ledum groenlandicum*, *Carex leptalea*, *Andromeda glaucophylla*, *Vaccinium oxycoccos*, and *Rubus pubescens*. Other mosses on the hummock included *Sphagnum magellanicum*, *Aulacomnium palustre*, *Pleurozium schreberi*, and *Dicranum undulatum*.

According to Vitt & Hamilton (1975), *Tomenthypnum falcifolium* appears to be endemic to boreal and subarctic zones of North America; they reported the species from scattered stations in British Columbia, Alberta, Manitoba, Ontario, Newfoundland, Quebec, New York, and Connecticut. It has also been reported from Michigan (Crum, 1976) and the Yukon (Vitt & Horton, 1979).

Itasca Co.: conifer swamp, near Grand Rapids, NW¼, NW¼, Sec. 21, T55N, R26W,
Wheeler & Glaser 5351 (MIN).

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THE HAMPTON CREEK WETLAND
COMPLEX IN SOUTHWESTERN MICHIGAN
III. STRUCTURE AND SUCCESSION OF TAMARACK FORESTS.

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The successional fate of forested peatlands in Michigan have intrigued ecologists for years. Working primarily in lowland conifer forests of northern Michigan, both Transeau (1903) and Gates (1942) had no problems in establishing a definite order of succession between these peatland communities and surrounding forest vegetation. In these northern areas "the bog societies are normally related to the conifer forests in their development to a climax tree vegetation" (Transeau, 1903). They saw evidence that northern lowland conifer forests develop as a result of invasion of high bog-shrub communities (or earlier associations) by *Larix laricina* (Tamarack), a deciduous conifer extremely intolerant of shade, followed by the more shade-tolerant *Picea mariana* (Black Spruce). This conifer society would then gradually give way to the climax forest society of *Acer saccharum* (Sugar Maple), *Fagus grandifolia* (Beech) and *Tsuga canadensis* (Hemlock). It is now apparent, though, that despite the floristic affinities evident between these northern peatlands and surrounding northern forest vegetation, the Black Spruce association is an edaphic climax and the peatland vegetation is not successional related to the upland forest vegetation (pers. comm. H. Crum).

Lowland conifer forest in southern Michigan, however, is neither floristically similar nor successional related to bordering regional climax hardwood forest. The floristic affinity of lowland conifer forest in southwestern Michigan (Brewer, 1966; Sytsma & Pippen, 1981b), as well as southeastern Wisconsin (Curtis, 1959), is closer to wet northern forest than the surrounding southern hardwood forest. One important species missing from these lowland conifer forests in southwestern Michigan, however, is Black Spruce, the shade-tolerant species necessary in forming the northern edaphic lowland climax forest. The information presented here on the structure and fate of wet northern forests in southwestern Michigan should be of interest since these forests lack the stabilizing presence of Black Spruce and since these forests show no apparent succession toward surrounding climax hardwood forests.

Three wet northern forests (hereafter referred to as Tamarack forests) representing distinct seres in lowland conifer forest succession were selected for analysis in the highly calcareous Hampton Creek wetland complex in Kalamazoo County (Sytsma & Pippen, 1981a, b). The three forests, all within 500 m of each other, border the meandering Hampton Creek (Fig. 1). The canopy, shrub,

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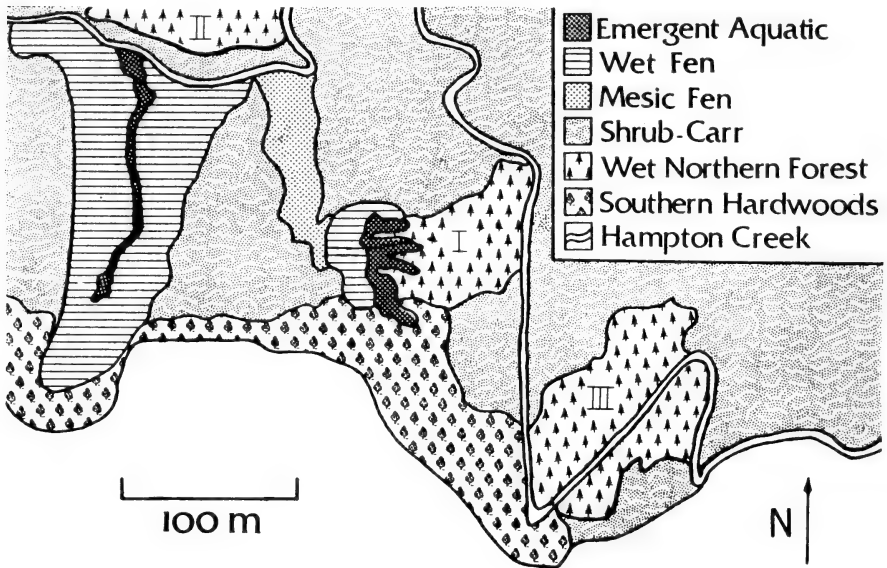


FIG. 1. Vegetation map of the tamarack forest study sites in the Hampton Creek wetland (I—young; II—mature; and III—old tamarack forests).

and herbaceous strata were sampled by nested quadrats in the summer of 1978. In each forest a grid composed of square quadrats, 5 m on a side, was laid out. Ten quadrats in the young and mature Tamarack forests and 12 quadrats in the old Tamarack forest were randomly selected. Species presence, density, and diameter at breast height of trees greater than 2.5 cm dbh were recorded for the entire 25 m² area of each quadrat. Species frequency, density, and dominance of each forest canopy were calculated. In a randomly chosen corner of each quadrat, 1 m² and 9 m² quadrats were sampled for herbs and shrubs (greater than 1 m tall, less than 2.5 m in diameter), respectively. Species presence and stem density were recorded for both the herbaceous and shrub strata. At the center of each forest, pH measurements and a peat core down to the marl sediments were obtained. Peat chemistry, except for pH, was fairly constant in each forest (Sytsma & Pippen, 1981a).

TAMARACK FOREST STRUCTURE

Young Tamarack Forest. The young Tamarack forest is located on a raised dome of peat about 65–80 cm above adjacent groundwater spring sites and Hampton Creek (Fig. 1). The forest is slowly invading the emergent aquatic and wet fen communities associated with the groundwater springs. It is situated on 2.95 m of peat, but only the top 5 cm are of woody origin. The forest floor is covered by a layer of Tamarack needles which are probably responsible for the acid nature of the surface peat (pH 4.4–5.0). Immediately below the surface,

the peat is circumneutral (pH 6.4). The forest presumably developed when Tamarack successfully invaded a shrubby fen that had existed for some time in the drainage basin of the spring sites since woody stems of *Potentilla fruticosa* (Shrubby Cinquefoil) and *Cornus stolonifera* (Red-osier Dogwood), both characteristic of fens in the wetland complex (Sytsma & Pippen, 1981b), can be readily identified in the top half meter of sedge/woody peat. Drainage from the groundwater springs to Hampton Creek has been impeded by the presence of the Tamarack forest, although drainage channels are now forming around its perimeter.

The canopy is almost completely dominated by *Larix laricina* (Table 1). An extraordinary number of small-diameter Tamaracks make this young forest almost impenetrable. Small trees (2.5–20 cm dbh) have a density of 6,280 trees/ha, while trees greater than 20 cm dbh have a density of only 40 trees/ha. *Toxicodendron vernix* (Poison Sumac) is scattered throughout the forest but only reaches subcanopy level. Two tall individuals of *Acer rubrum* (Red Maple) are also present. The shrub stratum is dominated by *Larix* saplings (including a large number that are dead), low bushes, and lianas (Table 2). The notable lack of high bush species is due to the extreme density of *Larix* and the shade it produces. The lack of a well-developed and diverse shrub stratum is reflected in the herbaceous layer. The six most abundant "herbs" are actually seedlings of potential shrub and canopy members (Table 3): *Lindera benzoin* (Spicebush), *Parthenocissus quinquefolia* (Virginia Creeper), *Toxicodendron vernix*, *Cornus stolonifera*, *Prunus serotina* (Wild Black Cherry), and *Amelanchier intermedia* (Juneberry). Characteristic true herbs include *Rubus pubescens* (Dwarf Red Raspberry), *Thelypteris palustris* (Marsh Fern), and *Viola pallens* (Smooth White Violet).

TABLE 1. Canopy and subcanopy composition and structure in young (I), mature (II), and old (III) tamarack forests.

	Frequency (%)			Density (no./ha)			Dominance (m ² /ha)		
	I	II	III	I	II	III	I	II	III
2.5–10 cm dbh									
<i>Larix laricina</i>	100	90	66.7	4720	2040	2033	16.4	7.1	5.6
<i>Toxicodendron vernix</i>	20	100	75.0	240	1760	1233	0.4	2.4	1.6
<i>Prunus serotina</i>	—	20	25.0	—	80	133	—	0.06	0.3
<i>Acer rubrum</i>	10	—	—	80	—	—	0.1	—	—
<i>Vitis riparia</i>	—	10	—	—	40	—	—	0.03	—
10–20 cm dbh									
<i>Larix laricina</i>	90	80	58.3	1560	600	566	16.4	7.7	8.8
20–30 cm dbh									
<i>Larix laricina</i>	10	40	16.7	40	240	67	2.5	10.9	2.8
30 cm dbh plus									
<i>Larix laricina</i>	—	—	33.3	—	—	200	—	—	21.0

TABLE 2. Relative frequency and density for the shrub stratum in young (I), mature (II), and old (III) tamarack forests.

	Relative Frequency (%)			Relative Density (%)		
	I	II	III	I	II	III
High Bushes & Saplings						
<i>Larix laricina</i>	23.3	5.1	8.3	55.7	21.5	9.6
<i>Toxicodendron vernix</i>	10.0	25.6	22.9	7.2	38.7	24.7
<i>Lindera benzoin</i>	3.3	—	25.0	2.4	—	33.7
<i>Cornus racemosa</i>	3.3	23.1	2.1	1.2	9.7	1.1
<i>Amelanchier intermedia</i>	3.3	7.7	4.2	0.6	2.2	3.4
<i>Vaccinium corymbosum</i>	—	2.6	6.3	—	5.4	6.2
<i>Prunus serotina</i>	—	5.1	2.1	—	2.2	1.1
<i>Acer rubrum</i>	—	—	4.2	—	—	4.5
<i>Aronia prunifolia</i>	—	5.1	—	—	3.2	—
<i>Cornus alternifolia</i>	—	—	4.2	—	—	3.4
<i>Ulmus rubra</i>	—	2.6	—	—	2.2	—
<i>Lonicera canadensis</i>	—	2.6	—	—	1.1	—
<i>Nemopanthus mucronatus</i>	—	—	2.1	—	—	0.6
Low Bushes						
<i>Cornus stolonifera</i>	6.7	—	4.2	5.4	—	4.5
<i>Betula pumila</i>	10.0	—	—	10.2	—	—
<i>Ribes hirtellum</i>	3.3	—	—	2.4	—	—
<i>Salix serissima</i>	3.3	—	—	1.2	—	—
Lianas						
<i>Parthenocissus quinquefolia</i>	20.0	10.3	8.3	7.8	8.6	5.6
<i>Toxicodendron radicans</i>	6.7	5.1	4.2	4.8	3.2	1.1
<i>Vitis riparia</i>	3.3	5.1	2.1	0.6	2.2	0.6
<i>Solanum dulcamara</i>	3.3	—	—	0.6	—	—

Mature Tamarack Forest. The mature Tamarack forest is separated from Hampton Creek by shrub-carr composed of *Cornus racemosa* (Gray Dogwood) and *Toxicodendron vernix* (Fig. 1). It is adjacent, however, to a sluggish inlet of Hampton Creek (not shown in Fig. 1) that allows the peat to remain wet throughout the year. The top 25 cm of the 2.1 m of peat is woody (pH 6.2–6.4). No evidence of shrub remains could be found near the top of the peat, although occasional small-diameter stem fragments were found lower in the peat profile with sedge peat.

The importance of *Larix* in the canopy is reduced when compared to the young Tamarack forest owing to the large increase of *Toxicodendron vernix* (Table 1). Only a half to a third of the number of small Tamaracks found in the young forest are present in the mature Tamarack forest, but a six-fold increase in the number of large Tamaracks offsets the reduction in density, thereby maintaining a closed canopy. Only a few individuals of *Prunus serotina* have successfully reached the canopy stratum. Unlike the young forest with mostly low bushes and lianas, only high bushes, saplings, and lianas are present in the mature Tamarack forest (Table 2). The prevalence of Poison Sumac and Gray

Dogwood in the shrub stratum might be exaggerated due to the presence of both species in adjacent shrub-carr. The herbaceous stratum is dominated by true herbs rather than shrub or tree seedlings as in the young Tamarack forest (Table 3). *Rubus pubescens*, *Viola cucullata* (Marsh Violet), *Lathyrus palustris* (Marsh Pea), *Senecio aureus* (Golden Ragwort), and *Symplocarpus foetidus* (Skunk Cabbage) are abundant in vegetative form but rarely flower. *Sphagnum fimbriatum* is confined to the bases of large Tamaracks.

TABLE 3. Percentage frequency of herbs occurring in at least 25% of the quadrats in young (I), mature (II), and old (III) tamarack forests. (Asterisks indicate frequencies less than 25%.)

	I	II	III
<i>Rubus pubescens</i>	66.6	100.0	100.0
<i>Parthenocissus quinquefolia</i>	91.6	83.3	91.6
<i>Thelypteris palustris</i>	66.6	41.7	75.0
<i>Lindera benzoin</i>	91.6	-----	83.7
<i>Viola cucullata</i>	25.0	83.3	66.6
<i>Toxicodendron vernix</i>	91.6	25.0	33.3
<i>Viola pallens</i>	58.3	25.0	58.3
<i>Galium aparine</i>	41.7	-----	91.6
<i>Senecio aureus</i>	****	75.0	58.3
<i>Solidago patula</i>	33.3	66.6	33.3
<i>Symplocarpus foetidus</i>	****	75.0	58.3
<i>Prunus serotina</i>	75.0	25.0	25.0
<i>Amelanchier intermedia</i>	66.6	25.0	25.0
<i>Galium triflorum</i>	58.3	58.3	-----
<i>Cornus stolonifera</i>	75.0	33.3	****
<i>Smilacina stellata</i>	25.0	50.0	33.3
<i>Maianthemum canadense</i>	-----	-----	91.6
<i>Aster puniceus</i>	-----	83.3	-----
<i>Scutellaria galericulata</i>	50.0	-----	33.3
<i>Trientalis borealis</i>	-----	****	83.3
<i>Cirsium muticum</i>	25.0	25.0	25.0
<i>Lathyrus palustris</i>	****	75.0	****
<i>Toxicodendron radicans</i>	****	25.0	50.0
<i>Oxypolis rigidior</i>	****	33.3	33.3
<i>Acer rubrum</i>	33.3	-----	25.0
<i>Cornus alternifolia</i>	33.3	-----	25.0
<i>C. racemosa</i>	****	33.3	-----
<i>Fragaria virginiana</i>	****	58.3	****
<i>Aster ericoides</i>	41.7	****	****
<i>Carex leptalea</i>	41.7	****	-----
<i>Krigia biflora</i>	33.3	-----	-----
<i>Poa trivialis</i>	33.3	-----	-----
<i>Circaea quadrisulcata</i>	-----	-----	33.3
<i>Polygonatum pubescens</i>	-----	-----	33.3
<i>Rudbeckia hirta</i>	25.0	-----	-----
<i>Vitis riparia</i>	25.0	-----	-----
<i>Lonicera canadensis</i>	-----	25.0	****
<i>Agrostis gigantea</i>	-----	25.0	-----
<i>Carex laevivaginata</i>	-----	25.0	-----
<i>Dryopteris clintonia</i>	-----	25.0	-----

Old Tamarack Forest. The latest seral stage of Tamarack forest succession evident in the Hampton Creek wetland complex is found in the northwestern section of a large Tamarack stand bisected by Hampton Creek (Fig. 1). The surface peat is slightly more acid than in the mature Tamarack forest (pH 6.0). Peat depth is only 2.47 m, but the peat does quake somewhat when several people walk on the central portion of the site. The quaking suggests that the peat might be slightly raised by hydrostatic pressure created by waterflow from Hampton Creek into or beneath the peat.

This Tamarack forest represents one of the last stages of Tamarack dominance in typical lowland conifer forest succession. The old age of the forest is made evident by the large number of fallen Tamaracks now covered by a variety of mosses. Seven percent of the Tamaracks, accounting for over 50% of the total stem basal area, are very large trees, greater than 30 cm in diameter (Table 1). Although the density of Tamaracks is similar to that in the mature Tamarack forest, there is a reduction in number of trees in all diameter size classes except the largest. This reduction is most evident in the intermediate class (20–30 cm dbh) and in the shrub stratum (Table 2). This structuring of size classes suggests that Tamarack is not replacing itself as in the younger forests. It does not appear, however, that deciduous trees are increasing at the expense of Tamarack since only a slight increase in density of deciduous canopy species is seen.

A two-fold increase in the density of shrubs in the old Tamarack forest ($1.2/\text{m}^2$) as compared to the mature Tamarack forest ($0.7/\text{m}^2$) is striking. Characteristic bog forest shrubs like *Toxicodendron vernix*, *Lindera benzoin* (Spicebush), *Vaccinium corymbosum* (Northern Highbush Blueberry), *Aronia prunifolia* (Red Chokeberry), and *Nemopanthes mucronatus* (Mountain Holly) are prevalent in the well-developed shrub stratum (Table 2). Herbaceous species typical of northern lowland forests include *Maianthemum canadense* (Wild Lily-of-the-Valley), *Trientalis borealis* (Star Flower), and *Viola pallens* (Smooth White Violet) (Table 3). *Cypripedium acaule* (Stemless Lady's Slipper), *Trillium cernuum* (Nodding Trillium), and *Sarracenia purpurea* (Pitcher Plant) are less common but characteristic of late stages in tamarack forest succession. *Sphagnum fimbriatum* is abundant in mounds at the base of Tamaracks or as blanket vegetation. Several genera of true mosses and liverworts including *Aulacomnium*, *Brachythecium*, *Conocephalum*, *Mnium*, and *Thuidium* are abundant and form extensive ground cover in many areas.

TAMARACK FOREST SUCCESSION

Tamarack seedlings successfully invade almost any wet peatland community where shrubs already present are too small or too widely spaced to shade them out (Dansereau & Segadas-Vianna, 1952). In highly calcareous glacial outwash plains like the Hampton Creek wetlands, Tamarack preferentially invades minerotrophic emergent aquatic or wet fen communities. The young forest, which developed after invasion of a shrubby fen, is now invading the hummocks surrounding the minerotrophic spring sites adjacent to the forest. In other areas of the wetland complex Tamarack is invading *Typha-Scirpus* and wet fen associations. The shallow-rooted Tamarack is restricted from the earlier

Chara sere because of its inability to gain a hold in soft, marly sediments. The drier condition of the upper peat layers in mesic fen and the dense canopy in *Cornus* shrub-carr also restrict Tamarack from these communities.

The minerotrophic condition of the sites where Tamarack successfully invades gives rise to dense stands of uniform-sized Tamarack. Low bushes grow best in these young dense forests. The herbaceous ground layer is dominated by species typical of shrub and canopy strata but unable to reach those strata under the existing low light conditions. Continued growth and natural thinning of the Tamaracks produce a diverse high shrub stratum at the expense of both small bushes and young Tamaracks. Increased light penetration to the forest floor allows lowland forest species like *Aster puniceus* (Purple-stemmed Aster), *Rubus pubescens*, *Senecio aureus* (Golden Ragwort), *Solidago patula* (Swamp Goldenrod), and *Symplocarpus foetidus* (Skunk Cabbage) to dominate the herbaceous groundlayer. Several species of true mosses and *Sphagnum* also appear with the increase in light penetration.

Further development of the forest results in a size-structured canopy dominated by large-diameter Tamaracks. Windthrows can be common in these old forests and might accelerate the evolution of the forest by raising its level (Dansereau & Segadas-Vianna, 1952). A marked decrease in the number of smaller Tamaracks, especially in the understory, along with an increase in the presence of high bog shrub species is typical of old tamarack forests. These changes in the shrub and canopy strata are accompanied by a change in the herbaceous composition from lowland forest species to northern forest (or even boreal forest) species. Both *Sphagnum* and feather mosses of various genera also become more important, especially the latter.

Further primary succession in Tamarack forests of southwestern Michigan typically involves the breaking of continuous conifer cover by deciduous species. Other deciduous species follow, quickly leading to the elimination of shade-intolerant Tamarack and a reduction in the amount and kind of shrubs in the understory. In Baroda Bog, Berrien County, similar to the Hampton Creek complex in calcareous nature and peat profile, Kurz (1928) observed the replacement of old Tamaracks by *Acer rubrum* (Red Maple), *A. saccharum* (Sugar Maple), *Fraxinus nigra* (Black Ash), and *Ulmus rubra* (Slippery Elm). Sugarloaf Bog, just south of the Hampton Creek wetland and in the same drainage basin, represents an advanced stage of this replacement. The forest there is dominated by *Betula alleghaniensis* (Yellow Birch), *Acer rubrum*, and *Pinus strobus* (White Pine), with Tamarack present only at very low density (Brewer, 1966). Similar replacements of Tamarack by southern hardwood species have been reported for northern Ohio (Sampson, 1930) and Cowles' Bog in Indiana (Kurz, 1923). Cowles' Bog is remarkably similar to Sugarloaf Bog, differing only in the additional presence of *Pinus banksiana* (Jack Pine) in the canopy. The low importance of southern hardwood forest species in the canopy and shrub strata of the old Tamarack forest, however, suggests that this replacement is not as rapid or as prevalent as usually believed. Although the importance of small-diameter Tamarack trees and saplings is greatly reduced in the old forest, Tamarack is abundant enough to fill any canopy gaps created by windthrows. Based on 100 years of land records in Kalamazoo County, Kenoyer (1930) stated that "the

swamp forest, including tamarack, is generally regarded as transient . . . but in the past century there has been no striking replacement of the swamp type." Transeau (1905) maintained that Tamarack forest in southern Michigan was a relic of former climatic conditions, and thus in the absence of disturbance no order of primary succession between the Tamarack and regional hardwood climax forests was to be expected. Alternatively, Brewer (1966) suggested that though Tamarack forest might eventually give rise to mixed forests like Sugarloaf Bog, disturbance by such agents as changing water levels, fires, and insect damage appears to be the prevalent fate of tamarack forest. Most of these disturbances lead to the replacement of the *Larix* association by earlier seral associations, which in turn can be invaded by new growth of Tamarack. Forests transitional between lowland conifer forest and bordering regional climax hardwood forest are apparently scarce in southern Michigan since Tamarack forest rarely remains undisturbed long enough to allow deciduous species to dominate the canopy. In the rare cases where disturbance is minimal, the transition to hardwood forest is probably so rapid that few examples of forests exhibiting the transitional stage have been recorded.

SUMMARY

The structure and succession of Tamarack forest in the Hampton Creek wetland complex, were studied by nested quadrats in 1978. Successional changes in the canopy, shrub, and herbaceous strata from young, dense forest stands to old, diverse stands are noted. Rapid successional development from Tamarack forest to southern hardwood forest is not evident. Tamarack appears to be replacing itself in canopy gaps despite its reduction in importance in the herbaceous and shrub strata of old forests. The apparent lack of transitional stages between the two forest associations is probably due to disturbance and the short duration of the intermediate stages.

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H THE TAXONOMY OF DRYOPTERIS X POYSERI WHERRY [7]

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The taxonomic intricacies of eastern North American woodferns, *Dryopteris*, are enough to give the average field botanist a headache. Of nearly 40 known kinds, more than two-thirds are sterile hybrids, some of them common and widespread, others rare and local. Pteridologists find them interesting because they constitute a superb example of a complex in which hybridization has produced a welter of diverse forms, including striking fertile crosses that reproduce and behave like normal species. They are thus interesting to a wide variety of botanists, including geographers, ecologists, morphologists, cytologists, and chemists. The final word on the relationships of these plants has by no means been said, and there are still many unanswered questions. The subject of eastern American *Dryopteris* was summarized more than a decade ago (W. Wagner, 1971), but since that time a number of new observations have been made, some not yet published.

The story of the problematic plant known as *Dryopteris* X *poyseri* Wherry began on 15 July 1906 when William Aldworth Poyser, of the Philadelphia area, collected some peculiar woodferns that appeared to be new to science. The plants were growing in a deep, shaded ravine in Swarthmore, Delaware Co., Pennsylvania, where they retained their unusual characteristics over several years. Poyser (*in* Clute, 1908) described his find as *Nephrodium cristatum clintonianum* fo. *silvaticum* and stated that it differed from typical *clintonianum* in the long-stalked pinnae "broader than in the normal form, as wide at base as in the middle; pinnules distant, linear-oblong, sharp-pointed, deeply serrate or toothed, the teeth often serrulate."

Shortly after Poyser's publication, Benedict (1909) gave a new interpretation of the plant. In an article entitled "New Hybrids in *Dryopteris*," Benedict came to the conclusion that forma *silvaticum* was actually a hybrid involving Goldie's Fern and Spinulose Woodfern. He gave it a formula name, *Dryopteris goldiana* X *spinulosa*, and there the matter rested for many years. Benedict's interpretation came largely from the characters given above, characters that do indeed resemble *D. goldiana*. However, relationship to *D. spinulosa* seemed less likely, in spite of Benedict's statement about "unmistakable *spinulosa* characters in the amount of cutting, in the unequally ovate-lanceolate lower pinnae, and the oblique habit of nearly all the pinnae, and in the position of the sori." Nevertheless, in 1960, Wherry took up Benedict's interpretation and gave the plant a binomial, naming it as a hybrid after the discoverer, *D. Xpoyseri* nom. nov.

¹Other herbarium specimens that show *poyseri*-like tendencies are (a) *Dryopteris boottii* abnormal? Cultivated at N.Y. Bot. Gard. R. C. Benedict 228 (NY); (b) *Dryopteris clintoniana*. Near Kamer, Albany Co., N.Y. E. G. Whitney 4057 (NYS).

Our own interest in the plant was stimulated by the fact that in spite of years of intensive effort, we had never succeeded in finding any hybrids of *D. goldiana* and *D. spinulosa*. That in itself is perhaps not surprising, because many of our fern hybrids are exceedingly rare. We were interested in studying the *goldiana* \times *spinulosa* hybrid in order to analyze the manner in which the parental characters interact, especially their chromosomes. Accordingly we borrowed Poyser's original specimen for study, continued our field searches for plants matching the alleged hybrid, and examined thousands of herbarium specimens (BH, CU, DUKE, GH, MICH, NY, NYS, PHIL, US).¹ The results are reported below.

Figures 1 and 2 show the upper and lower halves, respectively, of the holotype of *D. Xpoyseri* in the herbarium of the Philadelphia Academy of Sciences. The *goldiana*-like characters are immediately evident. However, the overall outline of the frond is obviously *not* like that of *goldiana*, nor is it like that of *spinulosa*, Benedict's other alleged parent. The frond outline is narrow and similar to normal *D. clintoniana*'s. It is interesting to note that Poyser himself in 1909, in an article on the fern flora of Pennsylvania, accepted Benedict's interpretation of his plant (listing it as *Nephrodium goldieanum* \times *spinulosum*) but wrote, "Neither alleged parent occurs in the immediate vicinity of the plants, and *goldieanum* [sic] not within several miles."

A specimen of Poyser's deposited in the American Fern Society herbarium (at the University of Michigan), although labeled "forma *sylvatica* Poyser," shows the diagnostic characters expressed only slightly. This specimen is illustrated in Fig. 3 (whole frond) and 4 (close-up of pinnae). Compared with Fig. 5, an "average" specimen of *D. clintoniana*, it is obvious that it is only slightly different. Clearly, in Poyser's opinion, his "forma *sylvaticum*" was only a variant of Clinton's woodfern, to which he originally referred it, and he was impressed by the fact that neither of Benedict's putative parental species grew at the Swarthmore locality. For this reason, we tended to agree with Poyser's original opinion (W. Wagner, 1971); however, we needed further confirmation.

In 1972 we had the good fortune to discover a very large and extensive population of *Dryopteris clintoniana* on property of Central Michigan University in Clare County (R5W, T17N, between sect. 16 and 17, 2.1 mi NW of the junction with Route 10 on the S side of Route 115). Here in swampy areas, *D. clintoniana* grows abundantly together with *D. intermedia* and *D. spinulosa* and occasional individuals of *D. marginalis*. A solitary plant (Wagner 72049, MICH—Figs. 6, 8, 9—lower) was discovered having the characteristics of *D. Xpoyseri* with these even more pronounced than in the type. The pinna stalks were very long, the segments well separated, narrow, and sharply pointed, and the margins strongly toothed. The sori were small and sporangia poorly developed. In the immediate vicinity of the unusual plant were numerous individuals of *D. clintoniana*, of which the plant in question was patently a mutant individual. Its characteristics were unlike those of any of the various well-known hybrids between the species of woodferns present at this locality. We tried to grow the plant in Ann Arbor, but it died. Thus we were unable to obtain data on chromosomes and spore development.

After several years, during a study of *Dryopteris* in the herbarium of Duke University, we encountered what is unquestionably a *bona fide* hybrid between

D. goldiana and *D. spinulosa*. It was discovered in 1937 in a bog near Monkton, Addison Co., Vermont, by D. S. and H. B. Correll. Its characteristics will be described in detail in a future paper, but salient contrasts with *poyseri* are given in Table 1. No other specimens that we have seen, either in the field or in the herbarium, so perfectly fit what this predicted hybrid should look like. The single specimen (*Correll 7799A*) is a beautiful frond—robust, complete, including sori and petiole base with scales. Superficially, it resembles a luxuriant individual of *D. spinulosa*, but features of pinna form (outlines, spacing of segments) confirm inheritance from *D. goldiana*. The tell-tale black and shining scales of the petiole base found in *D. goldiana* uniquely among North American woodferns show up conspicuously in the hybrid, thus leaving no question of its parentage. The plant is very different in appearance from *D. goldiana* \times *intermedia* (described in detail by Evans & W. Wagner, 1964). It should not be surprising that the Correll hybrid resembles *D. spinulosa* more than it does *D. goldiana*, as the former is a tetraploid taxon with $2n = 164$ chromosomes, and the latter is a diploid with $2n = 82$. Thus there is theoretically twice as much hereditary material from *D. spinulosa* as from *D. goldiana* with a consequently lop-sided influence from *spinulosa*. Field botanists are strongly encouraged to seek Correll's hybrid in new areas especially in New England and the Great Lakes region, where the parents commonly grow together. We warn that *D. goldiana* \times *spinulosa* can be readily overlooked because of its superficial resemblance to a large plant of *D. spinulosa*.

DISCUSSION AND CONCLUSIONS

The taxonomy of *Dryopteris* \times *poyseri* may now be confidently reinterpreted. The initial opinion of its discoverer is now confirmed. The plant is not the interspecific hybrid of *D. goldiana* and *D. spinulosa* as it was interpreted by Benedict & Wherry but an odd variant of *D. clintoniana*. Our evidence for this follows:

- a. Morphologically, transitions are found between the form originally illustrated (*in* Clute, 1908, p. 13, the model for which is evidently the pinna at the top of our Fig. 7) and normal *D. clintoniana* (Figs. 3, 4, 5).
- b. Similar, but even more extreme forms than the original collections have been found in Michigan with diagnostic characters much exaggerated (Figs. 6, 9 d-f).
- c. The habitat associations do not indicate origin by hybridization between *D. goldiana* and *D. spinulosa*. In fact, at the Pennsylvania locality neither of these species was present, and at the Michigan locality only *D. spinulosa* was present, although *D. clintoniana* was abundant.
- d. A *bona fide* hybrid *D. goldiana* \times *spinulosa* was discovered by the Corrells in Vermont, and a specimen of it is on deposit at Duke University. The morphology of this frond especially the basal scales accords accurately with what would be predicted in this hybrid combination, and it is strikingly different from that of *D. Xpoyseri* (see Table 1).

The fact that some of the characters of *D. Xpoyseri* are like those of *D. goldiana* is perhaps to be expected as *D. clintoniana* contains genomes of *D. goldiana*. It is now known that the normal form of *D. clintoniana* is itself of hybrid origin, with the cytogenetic formula of GGLSS, in which GG is the

GILL-LE



Fig. 1. Type specimen of *D. Xpoyseri* (PHIL), upper half of frond. (Scale in Fig. 6)



Fig. 2. Type specimen of *D. Xpoyseri* (PHIL), lower half of frond.



Fig. 3. Specimen labeled "*f. silvaticum* Poyser" showing only slight development of the distinctive characters.



Fig. 4. Specimen labeled "*f. silvaticum* Poyser" showing only slight development of the distinctive characters; enlargement showing pinna details. (Scale = 5 cm)



Fig. 5. Normal *D. clintoniana* from Clare Co., Mich. (Wagner 77139, MICH) (same locality as Fig. 6).



Fig. 6. Extreme *poyseri*-like form of *D. clintoniana*. Clare Co., Mich. (Wagner 72049, MICH). (Scale = 5 cm)

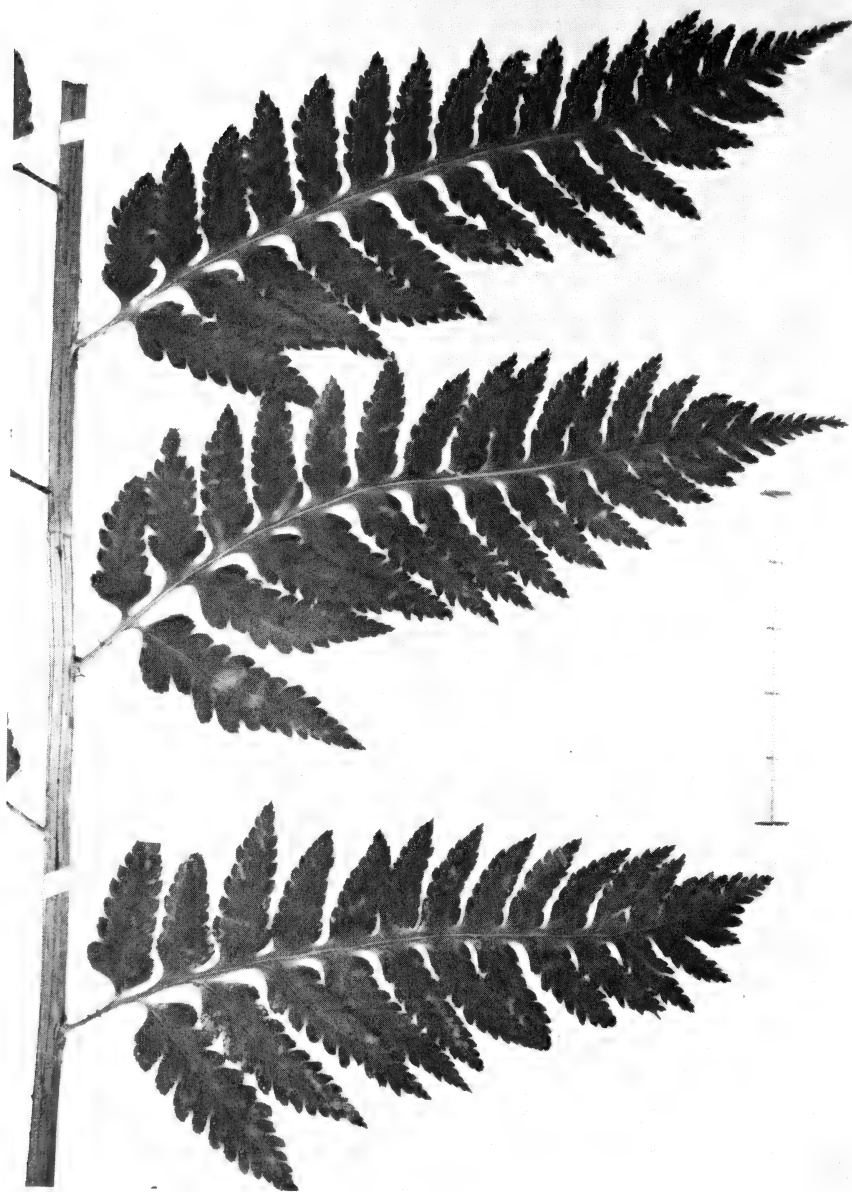


Fig. 7. Close up of pinnae of type specimen of *D. Xpoyseri* (PHIL). (Scale = 5 cm)



Fig. 8. Close up of pinnae of Michigan extreme *poyseri*-like form (Wagner 72049). Note very long pinna stalks; remote, narrow, sharp-pointed segments; and strongly toothed margins. (Scale = 5 cm)

TABLE 1. Comparisons of the type collection of *D. Xpoyseri* and *D. goldiana* \times *spinulosa* (Correll & Correll 7798a)

	poyseri	goldiana \times spinulosa
Scales of petiole base	Dull brown-gray	Shiny black
Blade cutting	More or less irregular	Regular and symmetrical
Medial pinna outline	Oblong, widest medially	Triangular-oblong, widest basally
Pinnule tips	Sharply pointed	Round-pointed to truncate
Pinnule margins	Finely and shallowly crenulate	Coarsely spinulose
Length of basal petiolules	10–12 mm	6–8 mm
Insertion of lower pinnules of basal pinnae	With stalks 1 mm long	Sessile to adnate

chromosome complement of *D. goldiana* and LLSS the complement of *D. cristata* (cf. W. Wagner, 1971). Sometime in the past, perhaps during or following glaciation, hybrids between the endemic diploid *D. goldiana* and the circumboreal *D. cristata* formed and doubled their chromosome numbers to produce a hexaploid sexual woodfern which now ranges from eastern Canada and New England to New Jersey and west to Michigan, where it is locally common in hardwood swamps. The range of *D. clintoniana* covers the area in which its parent species occur together most abundantly (T. Carlson, pers. comm.). Since *D. clintoniana* contains genes for the characters of *D. goldiana* and the plant discussed here is certainly a mutation of *D. clintoniana*, all we can conclude is that gene expressions of *D. goldiana* have been amplified in some way.

Although it should be obvious, we must make the nomenclatural caveat that the name *D. Xpoyseri* Wherry must not be applied to the real hybrid *D. goldiana* \times *spinulosa*. The type specimen of what was designated as *D. Xpoyseri* is a form of *D. clintoniana*, as its discoverer originally realized and as the observations reported above amply support. The binomial *D. Xpoyseri* is thus a taxonomic synonym of *D. clintoniana* f. *silvatica*.² If a binomial does come to be applied to the true hybrid *D. goldiana* \times *spinulosa*, it will have to be a new name. The name *poyseri* itself applies to a peculiar and trivial form of *D. clintoniana* which, as shown here, occurs sporadically, and is inconstant in expression. It does not deserve a scientific name.

This is part of continuing revisionary studies of North American *Dryopteris* supported by NSF Grant DEB75-03550. We wish to thank the curators of the herbaria of Duke University and the Philadelphia Academy of Science for their courtesies and the

²The first name was *Nephrodium cristatum clintonianum* f. *silvaticum* Poyser, but Clute (1908) anticipated future changes in the same article: "Recently there has been shown a disposition to consider *Clintonianum* a species distinct from *N. cristatum*. In that case the species would be *Nephrodium Clintonianum* and the form *N. Clintonianum silvaticum*. Those who prefer *Dryopteris* will of course call the form *Dryopteris Clintoniana silvatica*."

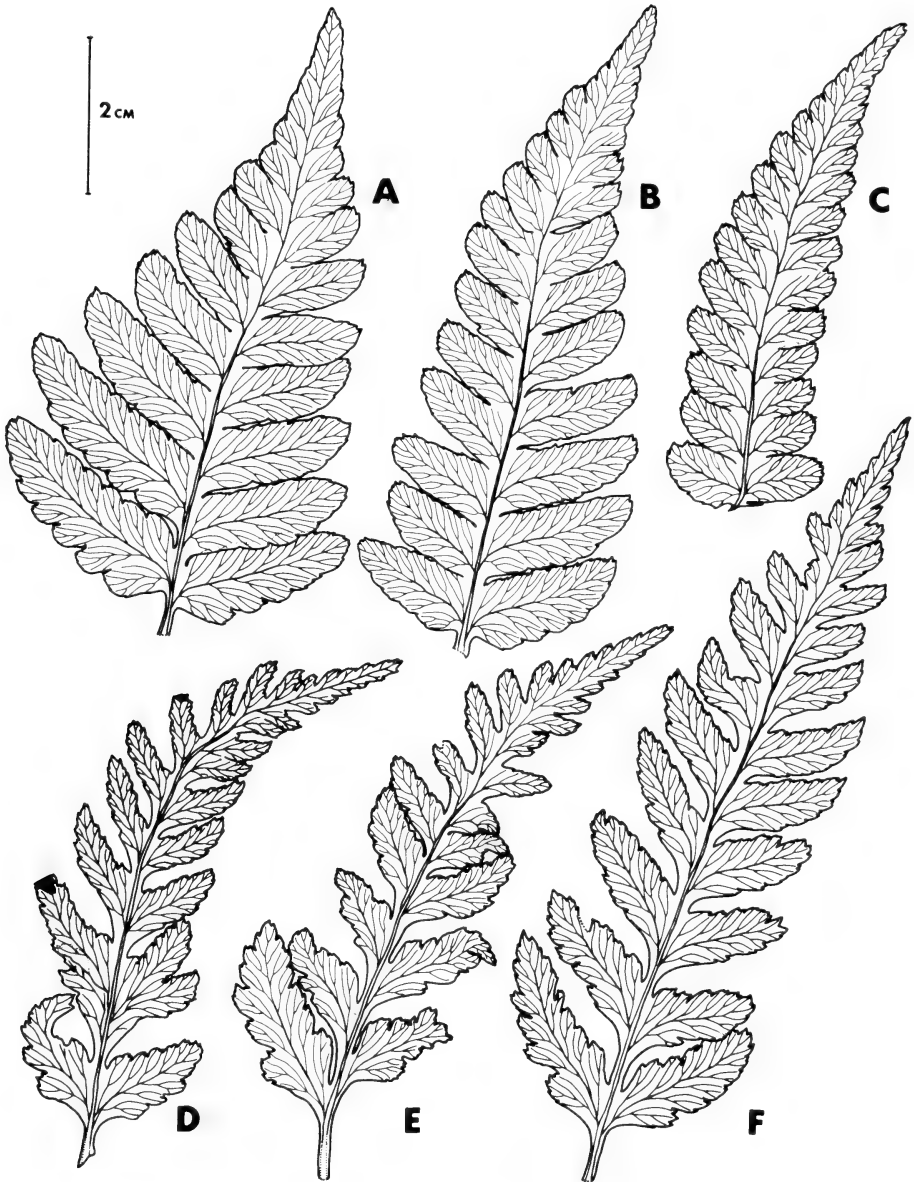


Fig. 9. Pinna patterns: A–C. *Dryopteris clintoniana* normal form (77139). D–F. Extreme *poyseri*-like form (72049). Note, in the latter, the very long petiolules; remote, narrow, sharp-pointed segments; and crenate margins.

following individuals for aid in various ways: D. S. Correll, T. F. Daniel, R. J. Hickey, J. G. Lacy, J. M. Beitel, K. S. Walter, and R. L. Wilbur.

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REVIEWS

THE SOUTHERN-MESIC FOREST OF SOUTHEASTERN WISCONSIN: SPECIES COMPOSITION AND COMMUNITY STRUCTURE. Milwaukee Public Museum, Contributions in Biology and Geology No. 41. By James B. Levenson. 1981. 246 pp. \$6.50 (paper) plus shipping (\$.90 domestic, \$1.40 foreign).

In the metropolitan Milwaukee area, 43 remnants of original southern mesic and southern dry-mesic forest (as described by Curtis) were studied in considerable detail in 1975. (Sites numbered 14, 18, & 22 are omitted in the individual descriptions, which begin with 1 and end with 46.) Tables present quantitative data on tree and shrub composition, and often groundlayer plants. A helpful feature is land-use history for each site where it could be determined. The precise information presented on location, geological situation, ownership, history, and composition of each site should make this a very useful work for teachers, naturalists, and those concerned with preservation of the best natural areas. Unfortunately it suffers from hasty editing and/or proofreading. And the pages seem to be perforated at the binding, making them easily detachable.

PRESETTLEMENT VEGETATION OF KALAMAZOO COUNTY, MICHIGAN. By Thomas W. Hodler, Richard Brewer, Lawrence G. Brewer, and Henry A. Raup. Department of Geography, Western Michigan University, Kalamazoo, Michigan 49008. 1981. map. \$2.00 plus shipping (\$.75 per order folded, \$2.75 per order rolled in tube).

On a scale of 1 inch to the mile, this map plots in 15 color shades the vegetation as of 1825–1830, based on notes of the original land surveyors. It is a grand and modern refinement of the work of Dr. L. A. Kenoyer half a century earlier. Unobtrusive gray lines indicate major presentday highways and borders of cities and villages, so that one may check contemporary localities although only township lines (not sections) are drawn. The 15 recognized vegetation types as well as the background of the map are explained in a marginal legend. A joint production of the departments of biology and geography at W. M. U., the map should be useful to biologists, historians, and others. It is available over-the-counter at the W. M. U. Campus Bookstore without the shipping charge.

—E. G. Voss

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 VASCULAR PLANTS OF THE
 RED LAKE PEATLAND, NORTHERN MINNESOTA [7]

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The Red Lake Peatland in northern Minnesota is the largest continuous peatland in the contiguous United States. The mire, covering an area of about 1200 km², consists of ombrotrophic bogs and minerotrophic fens assignable to four main areas: the Great Western Patterned Fen, the Divide, the Ludlow Patterned Fen, and the Koochiching Raised Bog Area (Wheeler & Glaser, 1979). Landforms include open bogs, wooded bogs, *Sphagnum* lawns, strings, flarks, fen pools, and wooded islands (Heinselman, 1963; Hofstetter, 1969; Griffin, 1977; Wheeler & Glaser, 1979). Partially dried-up fens and inundated drainage ditches have resulted from ditching and roadbuilding.

The peatland occupies a large area of gentle slope and poor drainage, and its flora is relatively impoverished. We found (in 1978) 195 vascular plants representative of 104 genera. When compared with other areas in Minnesota of similar (or smaller) size and climatic conditions, the depauperate nature of this flora is quickly realized. For example, a study (Wheeler, 1977) made about 160 km southeast in Itasca County and another (Moore, 1973) made in Anoka and Isanti Counties about 350 km south-southeast each recorded more than 700 species belonging to more than 300 genera.

The Asteraceae with eight genera and the Cyperaceae, Poaceae, and Orchidaceae each with seven genera have the largest representation. The Cyperaceae make up 25% of the taxa; *Carex* alone, with 29 taxa, makes up 15%. The next largest family, the Asteraceae, makes up 8%. Several vascular plants uncommon or rare in Minnesota have already been recorded (Wheeler & Glaser, 1979).

Major groups of the 195 plants found in the Red Lake Peatland

	Species		Genera	Families
	Native	Introduced		
Pteridophytes	7	0	6	3
Gymnosperms	4	0	4	2
Monocotyledons	81	0	32	12
Dicotyledons	101	2	62	33
Totals	193	2	104	50

The plants listed below include those found in the peatland proper and also at margins of drainage ditches in the interior and in partially dried-up fens adjacent to Highway 71 (a major highway that cuts through the Ludlow Patterned Fen). Not included are plants from marginal swamp communities, upland sites on mineral soil, wooded spoil banks near the highway, and roadside shoulders and embankments.—A complete set of voucher specimens is on deposit at the University of Minnesota Herbarium.

Habitat designations

- D – Disturbed Sites
 1 – Partially dried fens
 2 – Drainage ditches (including mar-
 gins)
 U – Found on most sites
 Q – Found on most minerotrophic sites and
 wooded islands
 T – Parasitic on *Picea mariana*

- O – Ombrotrophic Bogs
 1 – Open
 2 – Wooded
 M – Minerotrophic Fens
 1 – Narrow ecotone strips (poor fen)
 2 – *Sphagnum* lawns (poor fen)
 3 – Strings
 4 – Flarks and fen pools
 I – Wooded Islands
 1 – Undifferentiated
 2 – Hummocks
 3 – Hollows

EQUISETACEAE

- Equisetum fluviatile* L. M-4; D-2

OSMUNDACEAE

- Osmunda cinnamomea* L. I-2

POLYPODIACEAE

- Athyrium filix-femina* var. *michauxii*
 (Spreng.) Farwell I-2
Dryopteris cristata (L.) Gray M-3; I-2,
 D-1
D. spinulosa (Müller) Watt. I-2
Gymnocarpium dryopteris (L.) Newm.
 I-2
Thelypteris palustris var. *pubescens*
 (Lawson) Fern. Q

CUPRESSACEAE

- Thuja occidentalis* L. I-1

PINACEAE

- Larix laricina* (Du Roi) K. Koch U
Picea mariana (Mill.) BSP U
Pinus banksiana Lamb. D-2

APIACEAE

- Cicuta bulbifera* L. D-2
Sium suave Walt. D-2

APOCYNACEAE

- Apocynum cannabinum* L. D-2

ARACEAE

- Calla palustris* L. I-3; M-4

ASCLEPIADACEAE

- Asclepias incarnata* L. D-1

ASTERACEAE

- Aster junciformis* Rydb. M-3; M-1;
 D-1
A. puniceus L. I-2
A. umbellatus var. *pubens* Gray M-3;
 I-2; D-1
Bidens cernua L. D-1
B. connata var. *petiolata* (Nutt.) Farwell
 D-1
Cirsium arvense (L.) Scop. D-1
C. muticum Michx. I-2; M-3; D-1
Eupatorium maculatum L. D-1
E. perfoliatum L. D-1

- Petasites sagittatus* (Pursh) Gray I-2;
 D-1

- Senecio pauperculus* Michx. M-3; D-1

- Solidago canadensis* L. M-3; D-1

- S. graminifolia* (L.) Salisb. I-2; D-1

- S. uliginosa* Nutt. Q

- Sonchus arvensis* var. *glabrescens*
 Guenth. et al. I-2

BETULACEAE

- Alnus rugosa* (Du Roi) Spreng. D-2

- Betula papyrifera* Marsh D-2

- B. pumila* var. *glandulifera* Regel Q

- B. Xsandbergi* Britt. D-2

CAMPANULACEAE

- Campanula aparinoides* Pursh M-3; I-2;
 D-1

CAPRIFOLIACEAE

- Lonicera oblongifolia* (Goldie) Hook.
 I-2; D-1

- L. villosa* var. *solonis* (Eaton) Fern. I-2;
 D-1

- Viburnum trilobum* Marsh D-2

CARYOPHYLLACEAE

- Stellaria longifolia* Muhl. I-2; D-2

CORNACEAE

- Cornus canadensis* L. I-2

- C. rugosa* Lam. I-2

- C. stolonifera* Michx. I-3; M-3; D-1

CYPERACEAE

- Carex aquatilis* var. *altior* (Rydb.) Fern.
 D-2

- C. aurea* Nutt. D-2

- C. bebbii* Olney D-2

- C. brunnescens* var. *sphaerostachya*
 (Tuckerm.) Kükenth. I-2

- C. buxbaumii* Wahlenb. M-4; D-1

- C. canescens* var. *disjuncta* Fern. I-3;
 D-2

- C. cephalantha* (Bailey) Bickn. M-3;
 D-1

- C. chordorrhiza* L. f. Q

- C. diandra* Schrank I-3; D-2

- C. disperma* Dew. I-2

- C. exilis* Dew. M-1; M-3

- C. interior* Bailey D-1
C. lacustris Willd. D-2
C. lanuginosa Michx. D-2
C. lasiocarpa var. *americana* Fern. M-4; M-1; D-2; D-1
C. leptalea Wahlenb. M-4; I-3
C. limosa L. M-4; M-3; M-2; M-1; D-1
C. livida var. *grayana* (Dew.) Fern. M-4; M-2; M-1; D-1
C. oligosperma Michx. O-1; M-2
C. pauciflora Lightf. O-1; O-2; M-1
C. paupercula var. *pallens* Fern. O-2; M-1; I-2
C. projecta Mackenz. D-2
C. pseudo-cyperus L. I-3; D-2
C. rostrata var. *utriculata* (Boott) Bailey M-4; D-2
C. tenera Dew. D-2
C. tenuiflora Wahlenb. M-3; M-1; I-2; D-1
C. trisperma Dew. O-2; I-2
C. vaginata Tausch D-2
C. viridula Michx. D-2
Cladium mariscoides (Muhl.) Torr. M-4
Dulichium arundinaceum (L.) Britt. D-2
Eleocharis compressa Sulliv. M-4; D-1
Eriophorum angustifolium Honckeney M-4; D-1
E. chamissonis C. A. Meyer M-1; D-1
E. gracile Koch M-4
E. spissum Fern. O-1; O-2; M-1
E. tenellum Nutt. M-4
E. virginicum L. O-1; O-2; M-1
E. viridi-carinatum (Engelm.) Fern. M-4
Rhynchospora alba (L.) Vahl. M-4; M-1; D-1
R. fusca (L.) Ait. f. M-4
Scirpus atrocinctus Fern. D-1
S. cespitosus var. *callosus* Bigel. M-1; M-3
S. hudsonianus (Michx.) Fern. M-4; M-1; D-1
S. validus Vahl. M-4
DROSERACEAE
Drosera anglica Huds. M-4
D. intermedia Hayne M-4; M-1; D-1
D. linearis Goldie M-4
D. rotundifolia L. O-1; O-2; M-3; I-2; D-1
ERICACEAE
Andromeda glaucophylla Link U
Chamaedaphne calyculata (L.) Moench U
Gaultheria hispidula (L.) Bigel. O-2; I-2
Kalmia polifolia Wang. U
Ledum groenlandicum Oeder U
Vaccinium angustifolium Ait. I-2
V. myrtilloides Michx. O-1; O-2; I-2
V. oxycoccus L. U
V. vitis-idaea var. *minus* Lodd. O-2; I-2
GENTIANACEAE
Gentiana rubricaulis Schwein. D-1
Menyanthes trifoliata L. M-4; M-1; I-3
HIPPURIDACEAE
Hippuris vulgaris L. D-2
HYPERICACEAE
Hypericum virginicum var. *fraseri* (Spach) Fern. M-3; M-1; I-3; D-1
IRIDACEAE
Iris versicolor L. M-3; I-3; D-1
JUNCACEAE
Juncus alpinus var. *rariflorus* Hartm. D-1
J. brevicaudatus (Engelm.) Fern. D-2
J. canadensis J. Gay M-4; D-1
J. dudleyi Wieg. D-2
J. nodosus L. D-2
J. pelocarpus Mey. M-4
J. stygius var. *americanus* Buchenau M-4
JUNCAGINACEAE
Scheuchzeria palustris var. *americana* Fern. M-4; M-2; M-1
Triglochin maritima L. M-4; D-1
LAMIACEAE
Lycopus americanus Muhl. D-1
L. uniflorus Michx. M-3; I-2; D-1
Scutellaria epilobiifolia Hamilt. M-3; I-2; D-2
LENTIBULARIACEAE
Utricularia cornuta Michx. M-4
U. intermedia Hayne M-4; M-1; D-2
U. minor L. M-4
U. vulgaris L. D-2
LILIACEAE
Maianthemum canadense Desf. I-2
Smilacina trifolia (L.) Desf. O-2; I-2
LOBELIACEAE
Lobelia kalmii L. M-3; D-1
LORANTHACEAE
Arceuthobium pusillum Peck T
MYRICACEAE
Myrica gale L. I-3; D-1
NYMPHAEACEAE
Nuphar variegatum Engelm. D-2
ONAGRACEAE
Epilobium angustifolium L. D-2
E. leptophyllum Raf. M-3; I-2; D-1
ORCHIDACEAE
Arethusa bulbosa L. M-3
Cypripedium acaule Ait. O-2; I-2
Habenaria lacera (Michx.) Lodd. M-1; M-3; M-4
Liparis loeselii (L.) Rich. M-3
Listera cordata (L.) R. Br. O-2
Malaxis unifolia Michx. M-3
Pogonia ophioglossoides (L.) Ker M-4; M-3; M-1
P. ophioglossoides fo. *albiflora* Rand & Redfield M-4

POACEAE

- Agrostis scabra* Willd. I-2; M-3; D-1
Bromus ciliatus L. I-2; M-3; D-1
Calamagrostis canadensis (Michx.) Beauv. I-3; D-2
C. inexpansa var. *brevior* (Vasey) Stebbins D-2
C. neglecta (Ehrh.) Gaertn. I-3; D-2
Cinna latifolia (Trin.) Griseb. I-2
Glyceria borealis (Nash) Batchelder D-2
G. striata (Lam.) Hitchc. D-2
Muhlenbergia glomerata (Willd.) Trin. I-2; M-3; D-1
Phragmites communis var. *berlandieri* (Fourn.) Fern. M-4; D-1

POLYGONACEAE

- Polygonum sagittatum* L. I-2
Rumex orbiculatus Gray I-3

PRIMULACEAE

- Lysimachia terrestris* (L.) BSP D-1
L. thyrsiflora L. I-3; D-1
Trientalis borealis Raf. I-2; M-3

PYROLACEAE

- Monotropa uniflora* L. O-2; I-2
Pyrola asarifolia var. *purpurea* (Bunge) Fern. I-2
P. secunda var. *obtusata* Turcz. I-2

RANUNCULACEAE

- Caltha palustris* L. I-3; D-1
Ranunculus gmelini var. *hookeri* (D. Don) Benson I-3; D-2

RHAMNACEAE

- Rhamnus alnifolia* L'Her. M-3; I-2; D-1

ROSACEAE

- Amelanchier humilis* var. *compacta* Niels. I-2
Aronia melanocarpa (Michx.) Spach I-2
Geum aleppicum var. *strictum* (Ait.) Fern. I-2; D-1
Potentilla fruticosa L. M-3; M-1; D-1
P. palustris (L.) Scop. M-4; M-1; I-3; D-2
Rubus acaulis Michx. M-3; I-2; D-1
R. pubescens Raf. I-2; M-3; D-1
R. strigosus Michx. I-2; D-1

- Spiraea alba* Du Roi D-2

RUBIACEAE

- Galium labradoricum* Wieg. M-3; M-1; I-2; D-1

SALICACEAE

- Populus balsamifera* L. D-2
P. tremuloides Michx. D-2; I-2
Salix bebbiana Sarg. I-1; D-1
S. candida Fluegge I-1; D-1
S. discolor Muhl. I-1; D-1
S. gracilis Anderss. D-2
S. interior Rowlee D-2
S. lucida Muhl. D-2
S. pedicellaris var. *hypoglaucula* Fern. M-3; M-4; M-1; D-1
S. planifolia Pursh D-2
S. pyrifolia Anderss. I-2; D-1; D-2
S. serissima (Bailey) Fern. D-2

SARRACENIACEAE

- Sarracenia purpurea* L. U

SAXIFRAGACEAE

- Parnassia glauca* Raf. D-1
P. palustris var. *neogaea* Fern. M-3; M-4; M-1; D-1

SCROPHULARIACEAE

- Gerardia paupercula* var. *borealis* (Pennell) Deam D-1
Mimulus ringens L. D-2
Pedicularis lanceolata Michx. M-3; M-4; M-1; D-1

SPARGANIACEAE

- Sparganium minimum* (Hartm.) Fries I-3; D-2

TYPHACEAE

- Typha latifolia* L. M-4; I-3; D-2

VIOLACEAE

- Viola incognita* Brainerd I-2
V. pallens (Banks) Brainerd M-3; M-1; I-2; D-1
V. nephrophylla Greene D-1

XYRIDACEAE

- Xyris montana* Ries M-4

ZOSTERACEAE

- Potamogeton natans* L. I-3
P. gramineus L. M-4; I-3; D-2

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A NEW NORTHERN STATION FOR
TRIPHORA TRIANTHOPHORA [74]

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✓ ↓
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According to the literature (Case, 1964; Voss, 1972) and herbarium specimens, *Triphora trianthophora* (Nodding Pogonia, or Three-birds Orchid) indeed seems scarce and local. [Michigan] records have been confined to the southwestern and south-central part of the state, in Cass, Van Buren, Kalamazoo, Muskegon, and Ionia Counties, and there are unverified reports from Gratiot, Berrien, and Benzie Counties (Overlease & Overlease, 1975).



In August 1974, I found a colony of Nodding *Pogonia* in Leelanau County. Each year since plants have appeared in the same vicinity. The number of plants has varied from seven to perhaps more than 200, apparently depending on the amount of summer rainfall. The plants grow on the south slope of a large moraine in what is best described as a mixed deciduous forest dominated by beech and sugar maple and including groves of oak, cherry, paper birch and hemlock. An unusual feature of the colony is the presence of a number of *Triphora* plants under Big Tooth Aspen (*Populus grandidentata*). The tubers of the orchid grow in contact with sand below a 3-4 in. layer of leaf mold. The plants begin emerging about the first week of August, with the first blossoms two or three weeks later, and succeeding blossoms appear about weekly thereafter. While the 1978 season produced only about 50 plants, new locations were observed, both up and down the slope which had been carefully searched in previous years. The colony appears to be spreading.

Other orchids at this station include *Corallorhiza maculata*, *C. odontorhiza*, *Aplectrum hyemale*, and *Goodyera oblongifolia*. The adventive *Epipactis helleborine* is becoming common. It is interesting to note that *Corallorhiza odontorhiza*, the Autumn Coral-root, blooms here when the second or third *Triphora* blossoms of the season appear. This Coral-root is also north of its reported southern and central Michigan range.

I have placed voucher specimens in University of Michigan (MICH), Cranbrook (BLH), and U.S. National Herbaria (US).

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MICHIGAN PLANTS IN PRINT

A. MAPS, SOILS, GEOLOGY, CLIMATE, GENERAL (Continued)

- Barnes, James R., et al. 1979. Soil Survey of Ingham County, Michigan. U. S. Dep. Agr. 142 pp. + 84 folded map sheets + [5] folded sheets. [Replaces a survey done in 1933, published 1941.]
- Barnett, LeRoy. 1979. Milestones in Michigan mapping: Modern waymarks. Mich. History 63(6): 29-38. [A survey, with historical background, of various types of maps that have been produced, with references or addresses for further information on each.]
- Bowman, William L. 1981. Soil Survey of Monroe County, Michigan. U. S. Dep. Agr. 138 pp. + 87 folded map sheets + [5] folded sheets.
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MICHIGAN PLANTS IN PRINT

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On the cover: *The 1981 Spring Campout,*
McGulpin Point (the northernmost point of the
Lower Peninsula), E. G. Voss at center.
Photo by Clayton Alway

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THE

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May, 1982



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**MYTH AND FACT IN DETERMINING EDIBILITY
OF WILD PLANTS**

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How well do you really know the wild plants around you? Could you add wild food to your freeze-dried and canned foods on a camping trip? Could you feed yourself if you ever *really* became involved in a survival situation? Do you know some of the really tasty treats which the *cognoscenti* eat year-around for free? Are you supplementing your family menus with fresh wild foods? Do you know that children learn these plants easily—in much the same way fresh vegetables are learned in the grocery store?

Take the following quiz to see how prepared you are to “take to the woods.” The answers are followed by a discussion of some of the legitimate generalizations. There are exceptions to some of these true and false answers. If you are “in the know” for your area, give qualifying remarks and specific examples.

1. If birds or other animals eat a plant, it is okay for people to eat it—at least in small quantities.
2. If a plant has milky juice, it is poisonous.
3. If a plant stings your hands or mouth, don't eat it.
4. All blue-colored berries are edible.
5. No white-colored berries are edible.
6. All sumacs are poisonous.
7. Anything which looks like wild carrot (*Daucus carota*) should not be eaten.
8. If a plant is bitter, it is not fit for consumption.
9. Some parts of a wild plant may be edible while another part may be poisonous.
10. If properly prepared, some poisonous plants can be safely eaten.
11. All ferns are edible if dug when very young.
12. Pollutants do not harm wild plants due to their natural immunity.
13. If the edibility of a plant is unknown, take several bites every hour. If you do not become ill in eight hours, the plant is safe to eat in quantity.
14. The main reason that wild foods are not found in grocery stores is that they have no nutritional value.

ANSWERS

1. Not true. Many plants which animals and birds eat are not only unpalatable to humans but are actually poisonous. Poison ivy and poison sumac (*Rhus radicans* and *R. vernix*), relished by birds, can cause a painful dermatitis in many people. Birds also eat the berries of buckthorn (*Rhamnus catharticus*) which cause diarrhea in humans. Rodents eat the green fruit of May apples (*Podophyllum peltatum*) which cause severe cramping in humans. Podophyllin, the chemical found in May apples, is the main ingredient in Carter's Liver Pills.

2. Partially true. Some plants with milky juice are poisonous, such as Poinsettia, a member of the spurge family. One of the best edibles is milkweed, *Asclepias syriaca*, which has copious milky juice. Check a field guide to be cer-

tain of the identity of milkweed and dogbane (*Apocynum* sp.), which also has milky juice but causes stomach upsets.

3. Partially true. Common sense suggests not eating a stinging plant raw. However, one of the most nutritious, most common, and most tasty of our wild edibles is nettles (*Urtica dioica*) whose prickles are tamed by several minutes of immersion in boiling water. Prickly gooseberries (*Ribes* spp.) are inedible raw but also soften quickly in boiling water. Boil before using in pies, since baking does not completely soften the prickles.

4. Not true. Blueberries and huckleberries (*Vaccinium* spp. and *Gaylussacia* spp.) are edible, but many other blue-colored berries cause stomach upsets. Buckthorn (see no. 1) has blue-purple berries, and blue cohosh (*Caulophyllum thalictroides*) has poisonous vegetation and fruit which have caused death in children.

5. True for the most part. One exception is the sweet white mulberry (*Morus alba*). Several dogwoods (*Cornus* spp.) also have white fruit but are so insipid as to be classified as inedible.

6. Not true. The white-fruited sumacs are poisonous, with the fruits and vegetation causing a severe dermatitis in many people. All of the red-fruited sumacs are harmless, and their ripe fruiting heads make a nice tea and lemonade.

7. True unless you really can identify the fatally poisonous poison hemlock (*Conium maculatum*) and water hemlock (*Cicuta maculata*). Wild carrot (*Daucus carota*) is not especially good anyway—the roots tend to be woody unless dug when very young. Other wild plants in the parsley family (*Umbelliferae*) which are edible are the unexciting cow parsnip (*Heracleum lanatum*) and the exotic angelica (*Angelica archangelica*) of French liqueur.

8. Not completely true. Common sense dictates either to discard a bitter plant or to do something to tame the bitterness. Many onions (*Allium* spp.) are very strong; a second boiling or an initial sauté in butter or oil often cuts the strength. Bitter greens such as dandelions (*Taraxacum officinale*) and yellow rocket (*Barbarea vulgaris*), while appreciated by many people, often are quite strong in flavor. A second boiling makes them more palatable. Some vitamins will be lost, but many of these plants are already high in nutrients and will still be nourishing.

9. True. As with domestic vegetables, the wild plants have certain parts which are poisonous and others which are edible. Apple and cherry pits contain cyanide, for example, as do lima beans. Rhubarb leaves contain oxalic acid and a large serving of green-skinned potatoes contains one-tenth of the lethal dose of solanine. Collect pokeweed shoots when young (up to 12 inches high) and cook in at least two different waters. This dispels any poison which has a tendency to creep up from the extremely poisonous roots.

10. True. Marsh marigold (*Caltha palustris*) is the lovely, yellow-flowered, ditch-loving cowslip which contains helleborin, which is dispelled by immersion in boiling water. After boiling for several minutes, discard the water and complete the cooking in a second water. May apples when ripe are fine edibles, both raw and cooked. The rest of the plant remains poisonous. (See no. 1.)

11. False. Most ferns are inedible due to bitterness or poor texture. Fern croziers (the young fiddleheads) are not dug but are cut off at ground level when up to 6 inches high. Ostrich fern (*Matteuccia struthiopteris*) is a real gourmet

treat found along river banks; bracken fern (*Pteridium aquilinum*), the most common fern in North America, has often been used as an edible. However, Japanese research has found that the young shoots may be carcinogenic, especially when cooked in unsalted water. They are, nevertheless, still available in many Oriental food stores.

12. False. Wild plants are just as susceptible as domestic plants to harmful pollutants; check collecting localities carefully to avoid stream pollution, roadside lead poisoning, chemical pollutants, and weed killers. Check with the local road commission to determine which sprays are used along roadsides.

13. False. Death could occur early in this experiment; poison hemlock and water hemlock take their toll quickly.

14. False. Many wild plants are extremely high in nutrients. Many wild greens contain much higher levels of vitamin A than does spinach. One cup of rose hips (*Rosa* spp.) contains as much vitamin C as do two dozen oranges.

SOLID GENERALIZATIONS OF WILD EDIBILITY

Most of the mustards. The common mustards are recognized by the four-parted crucifer-type of flower, turgid, narrow seed pods, pungent taste, and leaves which have a terminal, rounded lobe below which are often pairs of small leaves. Examples are watercress (*Nasturtium officinale*), found in slowly moving water, yellow rocket (*Barbarea vulgaris*), the yellow mustard of fields, and the garlic mustard (*Alliaria officinalis*), a two-foot tall inhabitant of weedy, slightly moist ditches.

Sap of all the maples. In late winter and early spring when the nights are still cold and the days warm well above freezing, sap flows in maple trees (*Acer* spp.). This watery juice can be drunk "as is," used for vegetable cooking water, or boiled into syrup or sugar. Sugar maples (*A. saccharum*) are preferred due to their higher sugar content, although the ill-reputed box elder (*A. negundo*) produces a good quality of syrup as well.

All of the commonly recognized nuts. Okay to eat are the butternuts and walnuts (*Juglans cinerea* and *J. nigra*), hickories (*Carya* spp.), hazelnuts (*Corylus americana* and *C. cornuta*), and some species of acorns, especially in the white oak group (*Quercus alba* and *Q. macrocarpa*). The bitter tannin can be leached out by boiling in several waters or by placing in running water. The nuts should be completely ripe and if possible dried for several weeks to refine their taste and make them more gentle on the stomach.

Greens found in the garden. Many of the weeds found in gardens and other disturbed soil sites (such as vacant lots and construction dirt piles) have the potential for food. If picked clean when young and tender, the following plants make tasty, nutritious eating: lambs' quarters (*Chenopodium album*), pigweed (*Amaranthus* spp.), wild chives (*Allium schoenoprasum*), nettles (*Urtica dioica*), sheep sorrel (*Rumex acetosella*), and catnip (*Nepeta catarica*).

All of the onions. All of the onions (*Allium* spp.) are good for food and range from the skinny wild chives to the tangy wild garlics (*A. vineale*) and the gourmet wild leeks (*A. tricoccum*). Onions are recognized by appearance and smell. If the taste is too strong, they can be tamed by first sautéing in butter or by a second boiling. Be especially careful to avoid the deadly poisonous death

camus (*Zygadenus glaucus*) which resembles the onions but does not have the smell of an onion.

All of the commonly recognized berries. When ripe, most of the wild berries can be used raw or in the same jam, juice, or pie recipes as domestic varieties. These include both black and red raspberry (*Rubus occidentalis* and *R. strigosus*), blackberry (*R. allegheniensis*), mulberries (*Morus alba* and *M. rubra*), strawberry (*Fragaria virginica*), and thimbleberry (*R. parviflorus*). The leaves of these berry plants are also good both fresh and dried for tea. The leaves do not taste like the fruit but have a pleasant aroma and taste and contain no caffeine. Wild currents (*Ribes* spp.) also have good fruit, although the prickly texture of some of the gooseberries precludes eating them raw. Try pies and jams instead. Currant and gooseberry leaves are not used for tea.

Most of the conifer needles. Tea can be made from the needles of the conifers with the exception of the cedars (*Thuja* spp.), which can cause stomach problems. The conifer teas taste like turpentine or boiled Christmas trees. Fir needles, such as those of balsam fir (*Abies balsamea*), make a pleasant brew. Most parts of the yew (*Taxus* spp.) contain the poisonous alkaloid taxine and should not be eaten.

All of the common mints. Mints can be used for drinks, for flavoring, and for jelly. They have three good identifying features: a square stem when cut cross-wise, opposite leaves, and an obvious mint aroma when the leaves are bruised. Dry area mints are catnip (*Nepeta cataria*) and bee balm (*Monarda fistulosa*), which is also known as wild oregano and Oswego tea. There are many moist-area mints which grow along stream banks or right in the water. Two of the best of these are peppermint (*Mentha piperita*) and spearmint (*M. spicata*).

Three plants which are musts to learn for anyone even contemplating relying on native foods are cat tails (*Typha latifolia*), nettles (*Urtica dioica*), and the common milkweed (*Asclepias syriaca*). With the help of a good field guide (see below), these plants can easily be recognized and are found abundantly throughout the temperate areas. Do not eat day lilies (*Heimerocallis fulva*). These pretty orange and yellow roadside flowers have produced 150 known cases of severe stomach upsets during the past ten years (tubers, young shoots, young buds and flowers all have caused problems in Michigan, Ohio, Indiana, Ontario, and New York). Although lauded in many books as edible, they should certainly be avoided.

Since so many people, either on their own or through classes, are learning about—and using—wild plants as food, it is helpful to separate what are “old wives’ tales” and what are useful generalizations. By taking the patience to identify each plant properly, there are many tasty treats which freely await their harvesters.

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TETRAPLODON ANGUSTATUS IN MICHIGAN

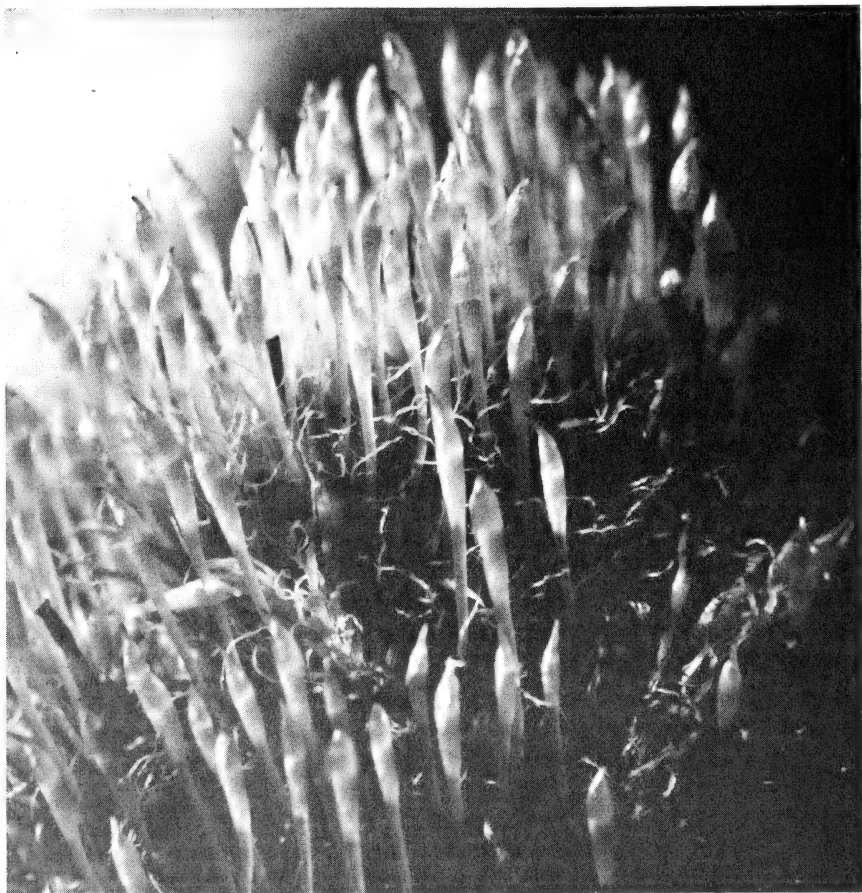
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Mosses of the family Splachnaceae tend to grow on dung and other organic substrates. Often these plants are noticeable because of elaborate, colorful capsules, most apparent in *Splachnum rubrum* and *S. luteum*. In both these species the hypophysis is enlarged, umbrella-shaped, and brightly colored, red and yellow, respectively. Several genera have capsules which are enlarged and unpleasantly scented; both characters have been suggested as ways of attracting insects for spore dispersal onto fresh organic substrates. *Tetraplodon*, less conspicuous than *Splachnum*, grows on the dung of carnivores, bones, and owl pellets. The capsules are unlike those of *Splachnum*, with the hypophysis elongate and narrower than the urn rather than broader. *Tetraplodon angustatus* has brown capsules, not or slightly exserted, and oblong-lanceolate, somewhat subulate, unevenly serrate leaves. It has a wide northern and montane distribution, in northern and central Europe, northern Italy, Siberia, China, Japan, Greenland, and northern North America. In the United States specimens have been collected in Maine, New Hampshire, New York, and Michigan. Two specimens have been reported from the Lake Superior region: one, from the herbarium of Dennis Cooley, was probably collected somewhere in the Upper Peninsula of Michigan, since William Burt, who supplied Cooley with many specimens, was a surveyor in the Upper Peninsula from 1840 to about 1850 (Voss, 1978) and probably collected this specimen at that time. The other specimen, collected by G. Loring in 1848 and labelled only Lake Superior region, was probably collected in Ontario, since Loring accompanied Agassiz on his expedition to the Canadian Shore of Lake Superior in the spring of 1848 (Voss, 1978).

On June 28, 1980 I found *Tetraplodon angustatus* in Summerby Swamp, in the southern part of the Upper Peninsula (Mackinac Co., Moran Twp., T41N, R4W, sect. 3, Streusand 520). Summerby Swamp has outskirts covered with dense *Thuja* swamp and an inner area of calcareous fen (pH 7.5–8.0) varying from open pools to *Sphagnum* hummocks covered with ericaceous shrubs to scattered clumps of trees, mostly *Thuja*, *Abies*, *Larix*, and *Picea mariana*. The vascular flora includes species of especially interesting distributions. *Empetrum nigrum* and *Erigeron hyssopifolius* reach their southern limits here. *Primula mistassinica*, *Juniperus horizontalis*, and *Pinguicula vulgaris* are northern species associated with the shores of the Great Lakes, but are found inland in this swamp. The bryophyte flora is equally interesting because of calciphiles such as *Scorpidium scorpioides*, *Catocopium nigrum*, *Hypnum pratense*, *Distichium inclinatum*, *Tomenthypnum nitens*, *Gymnostomum recurvirostrum*, *Drepanocladus vernicosus*, *Campylium stellatum*, and *Sphagnum warnstorffii*, northern species usually associated with beach pools in the Great Lakes area.

The *Tetraplodon* was found in a clump on a *Sphagnum* hummock (probably *S. warnstorffii*) at the side of an open pool of water (pH 7.5). The substrate was unrecognizable, but a large number of owl pellets were found in the swamp,



Tetraplodon angustatus in Mackinac Co.; photo by Jeffrey Holcombe.

probably from barred owls, the common swamp owls of the Upper Peninsula (R. Curry, pers. comm.). Next to the hummock was a dead tree with one branch extending over the hummock. Since some owls perch on snags when regurgitating pellets, it seems likely that the substrate of the *Tetraplodon* was an owl pellet. Another clump of *Tetraplodon angustatus* was found later in the summer by Nina Shishkoff, also among *Sphagnum* but in a more wooded part of Summerby Swamp.

Information on vascular plants and pH comes from Anna Weitzman. H. Crum, J. Holcombe, J. Rohrer, and N. Shishkoff helped to collect and identify bryophytes.

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**THE HAMPTON CREEK WETLAND COMPLEX
IN SOUTHWESTERN MICHIGAN
IV. FEN SUCCESSION**

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Peats or organic soils can form if the rate of deposition or accumulation of plant remains exceeds the rate of microbial breakdown of organic matter into minerals, water, and gases. Peatland formation involves a number of meteorological, physical, and chemical parameters but is controlled basically by climate, topography, and water availability (Boelter & Verry, 1977). Peats form best in the cool climates of northern latitudes and mountainous regions where precipitation exceeds transpiration. Though not restricted to areas modified by glacial activity, most peatlands are located on three glacial features: flat, morainal tills; sandy, outwash plains; and ice-block depressions or "kettles." Peat formation also requires an abundant supply of water in the form of precipitation, groundwater, or subsurface or surface flow through the peat.

The successional development of peatlands to climax communities in Michigan has interested investigators for years. One of the first detailed studies involving succession in Michigan peatlands is Transeau's (1905) work on bogs in the Huron River Valley. Other studies on Michigan bog peatlands, by Gates (1942), Brewer (1966), Crow (1969), Schwintzer & Williams (1974), and Schwintzer (1979), have added information about these systems. However, little work has been done on the floristics and succession of fen peatlands in Michigan.

Water source is an important criterion in distinguishing bog and fen peatlands. A bog has its primary water source from mineral-poor precipitation rather than from mineral-rich (largely calcium and magnesium) groundwater. These ombrotrophic ("rain-fed") peatlands are separated from the regional groundwater table either by the original topography of the glacial deposits or by extensive accumulations of *Sphagnum* peat. The absence of calcium, magnesium, and bicarbonate—the major buffering ion in natural aquatic systems—causes acid conditions to prevail in bogs. The dominance of *Sphagnum* mosses with their cation exchange and acid release mechanisms (Clymo, 1964) maintains the acidity of bog water, contributes to severe nutrient deficiencies, and reduces plant diversity (Heinselman, 1970). In contrast, a fen has its water source in mineral-rich groundwater. These minerotrophic ("mineral-fed") peatlands have relatively thin layers of sedge and graminoid peat isolating the fen vegetation from the regional groundwater table or from isolated sand aquifers. The groundwater frequently reaches the surface as springs that form a series of interconnecting hummocks and pools. Subsurface flow through the peat or surface flow

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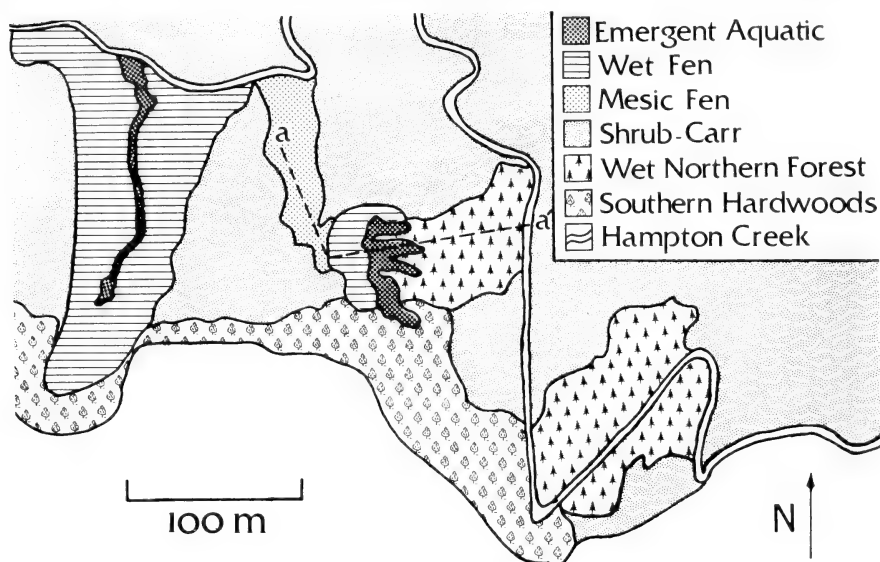


FIG. 1. Vegetation map of the fen study sites in the Hampton Creek wetland. Peat profile of transect a-a' through three of the major study sites and a young tamarack forest previously studied (Sytsma & Pippen, 1982) is shown in Fig. 3.

in drainage channels is maintained by the constant upward pressure of the groundwater flow. The high availability of nutrients and the presence of bicarbonate ions that maintain a neutral to slightly alkaline pH in fen water, allow for increased plant growth and diversity as compared to bogs.

The analysis presented here on fen peatland succession in the Hampton Creek wetland (Sytsma & Pippen, 1981a,b) was initiated in order to understand and encourage the preservation of a complex that harbors many rare and threatened plant species. These data should be of interest in view of the scarcity of such studies in Michigan and also helpful in the management and preservation of this and similar assemblages of rare and threatened plants found in fen peatlands in southern Michigan.

Four distinct fen seres were examined in the wetland complex (Fig. 1): (1) an emergent aquatic community associated with groundwater springs; (2) a wet fen community dominating the large depression where the springs are located; (3) a mesic fen community adjacent to the wet fen community and located on an elevated (1 m) area that is being invaded by shrub-carr; and (4) a marshy wet fen community located to the west of the other communities.

The emergent aquatic community and the fen communities were each sampled twice, in June and September 1978, by recording species present and stem density in 20 square-meter quadrats placed alternatively left to right along line transects. At all sites except the mesic fen, two permanently marked parallel 25 m transects were used with the quadrats spaced at 2.5 m intervals. The linearity of the mesic fen site necessitated using a single 50 m transect.

Peat cores down to the glacial sand were obtained for all sites with a David peat corer. The presence of marl sediments in the cores was tested in the field by applying HCl and noting the violence of the effervescence that resulted. The sites were surveyed with a Bruton Transit to determine changes in relief.

The physiography of the study area suggests that the peat is situated on a fairly level sandy outwash site with a slight depression where the groundwater springs are located (see Table 1 and Fig. 3). The peat elevation, however, is not at all level. The emergent aquatic site is the lowest point in the study area. The wet fen is situated in a bowl-shaped depression that slopes down to the emergent aquatic site from the 1 m elevated mesic fen site. Peat depth at the sites varies from a low of just under 1 m in the marshy wet fen to 3.5 m in the mesic fen (Table 1). An extensive layer of mixed sand and marl, averaging 35 cm deep, covers the glacial sand throughout all the sites. This marl has a sizable fraction of fragmented gastropod shells. The top meter of the mesic fen peat contains distinct thin layers of woody peat separated by large layers of sedge and graminoid peat. The source of the woody peat—either shrub or tree—could not be determined, although the small-diameter pieces suggest a shrub origin.

Emergent Aquatic Community. The emergent aquatic community site associated with the groundwater springs is a mosaic of peat hummocks and open pools. The water flows slowly southward and eastward around the invading wet northern forest in a series of narrow (1 m wide), interconnecting drainage channels before discharging into Hampton Creek farther east of the forest. The hummocks are formed by the clumping growth of the sedge *Carex stricta*. The hummocks are supported by sedge peat that gives them a springy character when walked on. The pools, however, underlain by 1 m of black, marly, aquatic peat, will not hold a person's weight. The CaCO_3 -precipitating *Chara* (Stonewort), *Scirpus acutus* (Hardstem Bulrush), and *Thelypteris palustris* (Marsh Fern) are dominant, with frequencies of 100% (Table 2). Several typical calciphiles, though not all abundant, include *Aster junciformis* (Bog Aster), *Gentiana procera* (Fringed Gentian), *Agalinis purpurea* (Purple Gerardia), *Solidago ohioensis* (Ohio Goldenrod), *S. uliginosa*, *Spiranthes cernua* (Nodding Ladies'-tresses),

TABLE 1. Physiography of fen communities in the Hampton Creek wetland.

	Elevation above sea level (m)	Peat Depth (m)	Peat Profile ¹
Emergent Aquatic	261.5	2.88	M-A-F
Wet Fen	261.65	2.77	M-S-F
Marshy Wet Fen	262.2- 263.1	1.51- 0.91	M-S-F
Mesic Fen	262.6	3.55	M-(W)-S-T

¹A = very fine, black, aquatic silt; F = nondecomposed fibrous peat; M = marl and sand (gray); S = decomposed sedge or graminoid peat (brown-black); T = black mineralized topsoil; W = woody peat.

TABLE 2. Frequency and stem density of vegetation in the emergent aquatic community.

	Frequency (%)	Density (no./m ²)		Frequency (%)	Density (no./m ²)
<i>Scirpus acutus</i>	100	15.4	<i>Juncus brachycephalus</i>	30	3.1
<i>Thelypteris palustris</i>	100	18.0	<i>Lathyrus palustris</i>	30	.6
<i>Campanula aparinoides</i>	90	9.7	<i>Pedicularis lanceolata</i>	30	.4
<i>Eupatorium maculatum</i>	90	3.6	<i>Calamagrostis canadensis</i>	25	1.2
<i>Aster junciformis</i>	85	3.3	<i>Carex hystericina</i>	25	.8
<i>Solidago patula</i>	85	2.8	<i>Rudbeckia hirta</i>	25	.5
<i>S. ohioensis</i>	80	3.3	<i>Senecio aureus</i>	25	2.2
<i>Cirsium muticum</i>	70	4.6	<i>Eriophorum viridi-carinatum</i>	20	.4
<i>Viola cucullata</i>	70	8.6	<i>Impatiens biflora</i>	20	1.2
<i>Carex stricta</i>	65	22.1	<i>Lobelia kalmii</i>	20	.6
<i>Potentilla fruticosa</i>	65	2.4	<i>Triglochin palustre</i>	20	.3
<i>Bromus ciliatus</i>	60	4.5	<i>Agalinis purpurea</i>	15	.2
<i>Lycopus americanus</i>	55	6.1	<i>Solidago canadensis</i>	15	.2
<i>Oxypolis rigidior</i>	55	2.0	<i>Spiranthes cernua</i>	15	.3
<i>Caltha palustris</i>	50	2.7	<i>Betula pumila</i>	10	.3
<i>Carex leptalea</i>	50	6.5	<i>Eleocharis erythropoda</i>	10	.7
<i>Carex prairea</i>	45	10.2	<i>Gentiana procera</i>	10	.2
<i>Solidago uliginosa</i>	45	2.7	<i>Larix laricina</i>	10	.1
<i>Drosera rotundifolia</i>	40	4.2	<i>Tofieldia glutinosa</i>	10	.4
<i>Eleocharis compressa</i>	40	31.4	<i>Toxicodendron vernix</i>	10	.1
<i>Typha latifolia</i>	40	1.8	<i>Apios americana</i>	5	.1
<i>Eupatorium perfoliatum</i>	35	.5	<i>Galium boreale</i>	5	.1
<i>Carex aquatilis</i>	30	2.4			

Tofieldia glutinosa (False Asphodel), and *Triglochin palustre* (Marsh Arrow Grass).

Wet Fen. The wet fen, which is situated in a bowl-shaped depression with the emergent aquatic community, is transitional between the groundwater springs and the elevated mesic fen. Standing water is not present, but the peat is saturated throughout the growing season and releases water when stepped upon. *Carex stricta* and *Thelypteris palustris* are dominant, along with the less frequent *Pycnanthemum virginianum* (Virginia Mountain Mint), *Rubus hispidus* (Swamp Dewberry), and *Solidago rugosa* (Rough-leaved Goldenrod) (Table 3). This combination of peat depth and depressed topography that gives rise to wet, calcareous conditions also allows the following more hydric fen species to reach their greatest development: *Aster puniceus* (Purple-stemmed Aster), *Bromus ciliatus* (Fringed Brome), *Carex prairea* (Prairie Sedge), *Iris virginica* (Blue Flag), *Monarda fistulosa* (Wild Bergamot), and *Potentilla fruticosa* (Shrubby Cinquefoil).

Mesic Fen. The greater distance from the groundwater springs and greater amount of peat separating the mesic fen vegetation from the groundwater table as compared to the adjacent wet fen enables an unusual assemblage of plants to exist in the mesic fen site. *Carex stricta*, *Pycnanthemum virginianum*, *Rubus hispidus*, and *Thelypteris palustris* are dominant as in the wet fen, but a large number of characteristic prairie species usually found on sandy or loamy soils instead of peat is also present (Table 4). *Andropogon gerardii* (Big Bluestem), *Liatriis spicata* (Blazing Star), *Silphium integrifolium* (Entire-leaved Rosinweed), *Solidago riddellii* (Prairie Goldenrod), and *Sorghastrum nutans* (Indian Grass) are a few representatives of this prairie element. The high frequency (60%) of

TABLE 3. Frequency and stem density of vegetation in the wet fen.

	Frequency (%)	Density (no./m ²)		Frequency (%)	Density (no./m ²)
<i>Carex stricta</i>	95	36.2	<i>Convolvulus americanus</i>	30	.7
<i>Thelypteris palustris</i>	80	14.7	<i>Krigia biflora</i>	30	.3
<i>Solidago rugosa</i>	75	6.1	<i>Sphenopholis intermedia</i>	30	1.0
<i>Pycnanthemum virginianum</i>	70	2.5	<i>Carex aquatilis</i>	25	5.6
<i>Rubus hispidus</i>	70	7.5	<i>Onoclea sensibilis</i>	25	1.1
<i>Monarda fistulosa</i>	65	4.9	<i>Galium boreale</i>	20	1.2
<i>Solidago canadensis</i>	65	5.4	<i>Impatiens biflora</i>	20	1.4
<i>Iris virginica</i>	60	1.8	<i>Poa palustris</i>	20	.8
<i>Smilacina stellata</i>	60	2.2	<i>Prunus serotina</i>	20	.8
<i>Zizia aurea</i>	60	3.5	<i>Agropyron trachycaulum</i>	15	.2
<i>Aster umbellatus</i>	55	1.0	<i>Aster novae-angliae</i>	15	.2
<i>Bromus ciliatus</i>	55	4.3	<i>Potentilla simplex</i>	15	.3
<i>Carex prairea</i>	55	19.6	<i>Typha latifolia</i>	15	.4
<i>Aster puniceus</i>	50	2.8	<i>Zigadenus glaucus</i>	15	.2
<i>Eupatorium maculatum</i>	50	1.9	<i>Apios americana</i>	10	.1
<i>Fragaria virginiana</i>	50	3.0	<i>Caltha palustris</i>	10	.2
<i>Phlox pilosa</i>	50	1.5	<i>Cicuta bulbifera</i>	10	.2
<i>Potentilla fruticosa</i>	50	2.6	<i>Oenothera parviflora</i>	10	.1
<i>Sorghastrum nutans</i>	50	2.1	<i>Pedicularis lanceolata</i>	10	.1
<i>Thalictrum dasycarpum</i>	50	2.1	<i>Geranium maculatum</i>	5	.1
<i>Cirsium muticum</i>	45	4.0	<i>Lycopus americanus</i>	5	.2
<i>Cornus racemosa</i>	45	1.3	<i>Muhlenbergia glomerata</i>	5	.1
<i>Lathyrus palustris</i>	45	1.1	<i>Scirpus acutus</i>	5	.1
<i>Osmunda regalis</i>	40	.9	<i>Scutellaria galericulata</i>	5	.2

TABLE 4. Frequency and stem density of vegetation in the mesic fen.

	Frequency (%)	Density (no./m ²)		Frequency (%)	Density (no./m ²)
<i>Carex stricta</i>	90	28.4	<i>Andropogon gerardii</i>	25	1.5
<i>Potentilla simplex</i>	70	4.8	<i>Geranium maculatum</i>	25	.4
<i>Pycnanthemum virginianum</i>	70	3.7	<i>Phlox pilosa</i>	25	.8
<i>Rubus hispidus</i>	70	2.9	<i>Monarda fistulosa</i>	20	.5
<i>Smilacina stellata</i>	65	1.7	<i>Onoclea sensibilis</i>	20	1.1
<i>Thelypteris palustris</i>	65	9.3	<i>Populus tremuloides</i>	20	.2
<i>Cornus racemosa</i>	60	.9	<i>Toxicodendron vernix</i>	20	.4
<i>Lathyrus palustris</i>	60	1.5	<i>Liatris spicata</i>	15	.4
<i>Osmunda regalis</i>	55	1.4	<i>Panicum boreale</i>	15	.6
<i>Sorghastrum nutans</i>	55	2.5	<i>Verbena hastata</i>	15	.3
<i>Thalictrum dasycarpum</i>	55	.9	<i>Helianthus giganteus</i>	10	.1
<i>Zizia aurea</i>	50	1.2	<i>Krigia biflora</i>	10	.2
<i>Potentilla fruticosa</i>	45	2.3	<i>Silphium integrifolium</i>	10	.3
<i>Eupatorium maculatum</i>	40	1.0	<i>Solidago rugosa</i>	10	.2
<i>Fragaria virginiana</i>	40	1.7	<i>Asclepias syriaca</i>	5	.1
<i>Galium boreale</i>	40	2.1	<i>Castilleja coccinea</i>	5	.1
<i>Stellaria longifolia</i>	40	.9	<i>Comandra umbellata</i>	5	.3
<i>Aster umbellatus</i>	35	1.0	<i>Convolvulus americanus</i>	5	.2
<i>Cirsium muticum</i>	35	1.3	<i>Gentiana andrewsii</i>	5	.1
<i>Poa alsodes</i>	30	1.2	<i>Iris virginica</i>	5	.1
<i>Prunus serotina</i>	30	.8	<i>Solidago riddellii</i>	5	.2
<i>Veronicastrum virginicum</i>	30	.8	<i>Spartina pectinata</i>	5	.1

Cornus racemosa (Gray Dogwood) is significant since the mesic fen site is completely surrounded by shrub-carr composed of *C. racemosa* clones. It suggests future invasion of the mesic fen site by shrub-carr.

An unusual characteristic of this mesic fen is a strip of Shrubby Cinquefoil down the middle of the site. Associated with this shrub are other mesic fen species like *Lathyrus palustris* (Marsh Pea), *Smilacina stellata* (Starry False Solomon's-seal), and *Thelypteris palustris*. Since the transect was placed near the middle of the site, the frequencies of these species are exaggerated (see Table 4). The presence of this vegetation strip indicates greater moisture availability and suggests subsurface drainage through the peat.

Marshy Wet Fen. This wet fen is located on a sloping (55 cm/100 m) and shallow peatland area between elevated groundwater springs and Hampton Creek. This fen is thus inundated by slowly flowing groundwater that drains in a series of channels formed by interconnecting sedge hummocks. As in the previously discussed wet fen, *Carex stricta* and *Thelypteris palustris* are dominant (Table 5). The high frequency and density measures for *Aster lucidulus* (Glossy-leaved Aster), *Calamagrostis canadensis* (Blue-joint), *Campanula aparinoides*

TABLE 5. Frequency and stem density of vegetation in the young wet fen.

	Frequency (%)	Density (no./m ²)		Frequency (%)	Density (no./m ²)
<i>Carex stricta</i>	100	30.7	<i>Apios americana</i>	10	.1
<i>Thelypteris palustris</i>	100	18.3	<i>Berula erecta</i>	10	.4
<i>Eupatorium maculatum</i>	70	3.1	<i>Calamagrostis stricta</i>	10	.3
<i>Aster lucidulus</i>	65	6.5	<i>Eleocharis elliptica</i>	10	5.4
<i>Solidago rugosa</i>	65	5.1	<i>Galium boreale</i>	10	.2
<i>Calamagrostis canadensis</i>	60	7.7	<i>Impatiens biflora</i>	10	.4
<i>Carex prairea</i>	60	7.4	<i>Oxypolis rigidior</i>	10	.2
<i>Onoclea sensibilis</i>	55	2.0	<i>Solidago ohioensis</i>	10	.3
<i>Lycopus americanus</i>	50	4.9	<i>Sorghastrum nutans</i>	10	.3
<i>Campanula aparinoides</i>	45	3.8	<i>Angelica atropurpurea</i>	5	.1
<i>Lemna minor</i>	45	29.1	<i>Asclepias incarnata</i>	5	.2
<i>Bromus ciliatus</i>	35	2.7	<i>Aster novae-angliae</i>	5	.1
<i>Caltha palustris</i>	35	1.5	<i>Cacalia plantaginea</i>	5	.2
<i>Potentilla fruticosa</i>	35	.8	<i>Carex aquatilis</i>	5	.1
<i>Cirsium muticum</i>	30	.9	<i>C. buxbaumii</i>	5	.1
<i>Agrostis gigantea</i>	25	.8	<i>C. hystericina</i>	5	.3
<i>Spiraea alba</i>	25	.3	<i>C. leptalea</i>	5	.2
<i>Utricularia intermedia</i>	25	.4	<i>Epilobium strictum</i>	5	.1
<i>Cornus stolonifera</i>	20	.6	<i>Helianthus giganteus</i>	5	.1
<i>Fragaria virginiana</i>	20	.2	<i>Juncus nodosus</i>	5	1.2
<i>Pycnanthemum virginianum</i>	20	.4	<i>Muhlenbergia mexicana</i>	5	.1
<i>Rubus hispidus</i>	20	.4	<i>Pedicularis lanceolata</i>	5	.1
<i>Solidago patula</i>	20	.3	<i>Populus tremuloides</i>	5	.1
<i>Cicuta bulbifera</i>	15	.2	<i>Prunus serotina</i>	5	.2
<i>Lathyrus palustris</i>	15	.2	<i>Rosa palustris</i>	5	.1
<i>Monarda fistulosa</i>	15	.2	<i>Rumex orbiculatus</i>	5	.1
<i>Nasturtium officinale</i>	15	2.8	<i>Salix serissima</i>	5	.1
<i>Poa alsodes</i>	15	.2	<i>Smilacina stellata</i>	5	.2
<i>Polygonum sagittatum</i>	15	.4	<i>Solidago uliginosa</i>	5	.1
<i>Scutellaria galericulata</i>	15	.3	<i>Symplocarpus foetidus</i>	5	.1
<i>Typha latifolia</i>	15	.5	<i>Thalictrum dasycarpum</i>	5	.1
<i>Viola cucullata</i>	15	.6			

(Blue Marsh Bellflower), and *Lycopus americanus* (Water Horehound) are indicative of the marshy conditions prevalent at this fen site. A metallic sheen over most of the stagnant water pools indicates the abundance of iron-fixing bacteria.

Fen Succession

Successional Rates. The presence of an underlying layer of marl sediments with disintegrated gastropod shells at all the study sites indicates that this area of the Hampton Creek wetland complex was under water by the time the glaciers retreated from the area—approximately 12,000 years ago (Martin, 1957). Meltwater from the Kalamazoo lateral moraines located farther west in Oshtemo and Texas Townships formed the sandy, outwash depression now occupied by the peatland complex. Hampton Lake, the ice-block-formed “kettle” lake one-half kilometer east of the study sites, presumably blocked the meltwater sufficiently to cause ponding upstream. Even to this day drainage from Hampton Lake is poor. The shallow lake formed by meltwater was then open to invasion and modification by aquatic plants and algae. The 35 cm depth of marl of the study sites probably was deposited quickly by *Chara*, blue-green algae, and invertebrates inhabiting the cold and highly alkaline shallow lake.

The sedge and graminoid peat formed from the growth of emergent aquatic plants later covered the marl sediments. The rate of peat production is difficult to ascertain. Estimates in the southern Great Lakes region vary from 100 years per foot in moss-dominated systems to 800 years per foot in sedge- or graminoid-dominated systems (Curtis, 1959). Peat production during primary hydrarch succession in cold alkaline lakes in the Erie Basin has been estimated between 240 and 360 years per foot (Sears & Janson, 1933). Using 360 and 800 as the probable range for rates of peat production in fen systems where sedge peat is very compressed, the maximum peat depth of 3.5 m in the mesic fen would have taken between 4,200 and 9,000 years to accumulate—or roughly one-half to three-fourths of the time available since the retreat of the last glaciers.

These indications of rates must be used with caution, however, since adjacent and similar peatlands can show marked differences in peat accumulation (Curtis, 1959). The difference in peat depth between the wet fen and the marshy wet fen (see Table 1) is striking even though both presumably originated at the same time and are separated by only 75 m of shrub-carr. Two features of this marshy wet fen site are probably responsible for its slower development. The groundwater enters the fen site at the most elevated end of the fen and then flows down a sloping incline before draining into Hampton Creek. Peat has not accumulated quickly in this fen site because of increased water flow caused by the combination of elevated groundwater springs and sloping incline. However, near Hampton Creek where the water flow is considerably slower, peat has accumulated to a greater depth. This example indicates that minute changes in relief, water movement, and water chemistry can drastically alter the rate of peat formation (Boetter & Verry, 1977).

Successional Directions. The general sequence of peatland succession in the fen sites as evidenced by our peat profiles is (1) aquatic marl sedimentation

following meltwater ponding about 10,000-11,000 years ago; (2) the development of marsh and fen communities beginning between 4,200 and 9,000 years ago and continuing to the present; (3) the periodic invasion of shrub-carr during warmer and drier intervals in the last 4,000 years and now spreading in the areas with the deepest peat accumulation; and (4) the recent invasion by wet northern forest in the more minerotrophic emergent aquatic sites and their drainage channels.

The successional relationships among the plant associations in the Hampton Creek wetland complex are shown in Fig. 2. The *Chara* association of aquatic plants and algae deposit the marl sediments upon which the *Typha-Scirpus* emergent aquatic association eventually grows. The *Calamagrostis* association of marsh grasses invades the *Typha-Scirpus* association when a sufficient amount of deposited organic or mineral material elevates the soil layer at or above the water level. If a hard groundwater source is maintained, a calciphilic fen association of hydric forbs and grasses replaces the *Calamagrostis* marsh association.

With increasing peat accumulation to 3 m and the subsequent isolation of the vegetation from the groundwater, the wet fen community is quickly invaded by the *Cornus* shrub-carr association (Curtis, 1959). Where the fen community is not invaded by shrub-carr, the drier conditions allow the mesic fen association with its unusual assemblage of prairie species to develop. This mesic fen bears a

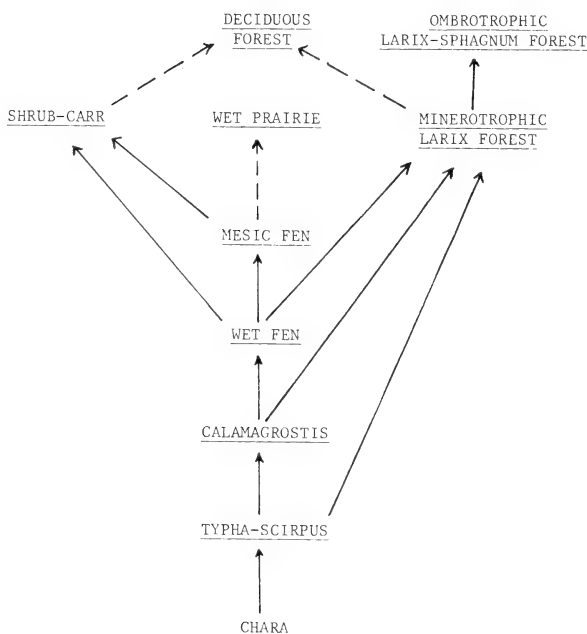


FIG. 2. Successional trends among the plant associations in the Hampton Creek wetland. Dashed arrows indicate possible but not apparent trends. (Based partly on Sytsma & Pippen, 1982).

close floristic relationship to wet prairie communities (see Brewer, 1965), and it has been suggested that fens in the southern Great Lakes region are merely variants of moist soil prairies with internal water sources (Curtis, 1959). This relationship is emphasized by the possibility that wet prairies, like fens, are derived from glacial marshes (Kenoyer, 1930; Brewer, 1965). With increased peat accumulation, further isolation of the vegetation from the groundwater, and subsequent mineralization of the top peat layers in the mesic fen, it is probable that a wet prairie community could become established before shrub-carr completely invades the fen sites.

Future Succession. Two dominant trends, based on interpretation of aerial photographs dating back 20 years, can be seen in the future succession of the peatlands in the Hampton Creek wetland complex. The first is the rapid invasion of drier peat areas by shrub-carr (Fig. 3). Most of the study site is covered by 2-3 m of peat, the maximum depth that Heinzelman (1970) suggested for minerotrophic peat development. Curtis (1959) pointed out that in Wisconsin the expansion of shrub-carr was greatest in wetlands protected by the Conservation Department for Public Hunting and Fishing Grounds and also mentioned that attempts to drain peatlands by dredging channels or by enlarging natural outlets caused the surface layer of the peat to oxidize and form a mucky, black, organic soil favorable for shrub-carr invasion. Undoubtedly, attempts to drain the peat and the absence of either fire or mowing in the Hampton Creek wetland complex (due to protection by the Department of Natural Resources) have accelerated this replacement of fen vegetation by shrub-carr. Shrub-carr is highly stable; 50 years is considered the minimum life-span for shrub-carr dominance of peatland sites (White, 1965). Cain & Slater (1948) stated that the fate of shrub-carr is to be replaced by deciduous forest, but the ability of *Cornus racemosa* to reproduce asexually and the extreme shading produced by this cloning have prevented many of the deciduous forest species from becoming established.

The second trend is the spread of wet northern forest into emergent aquatic and wet fen sites. The minerotrophic condition of these fen sites gives rise to rich stands of Tamarack (Sytsma & Pippen, 1982). Through time, however, the eventual plugging of groundwater springs by accumulated sand and aquatic peat and the isolation of vegetation from subsurface groundwater flow by increased deposition of woody and sedge/*Sphagnum* peat could cause a shift in water sources from nutrient-rich groundwater to nutrient-poor precipitation.

Heinzelman (1970) has pointed out that in the Agassiz Peatlands Natural Area in Minnesota peatland evolution does not necessarily fit the conventional concept of succession towards mesophytism, terrestrialization, and uniformity with peat accumulation (e.g. Gates, 1942). As seen now in the Hampton Creek wetland complex, a similar trend is evident towards landscape diversity with emergent aquatic sites, young fens, mesic fens, shrub-carr, and wet northern forests developing in close juxtaposition. However, if the dominance of shrub-carr and wet northern forest continues, as indicated by interpretation of aerial photographs, many of these diverse community types, especially fens, might disappear. Undoubtedly, the influence of people in the cessation of natural fires and the lowering of the regional groundwater table have been and will continue to be instrumental in the succession of this unique peatland.

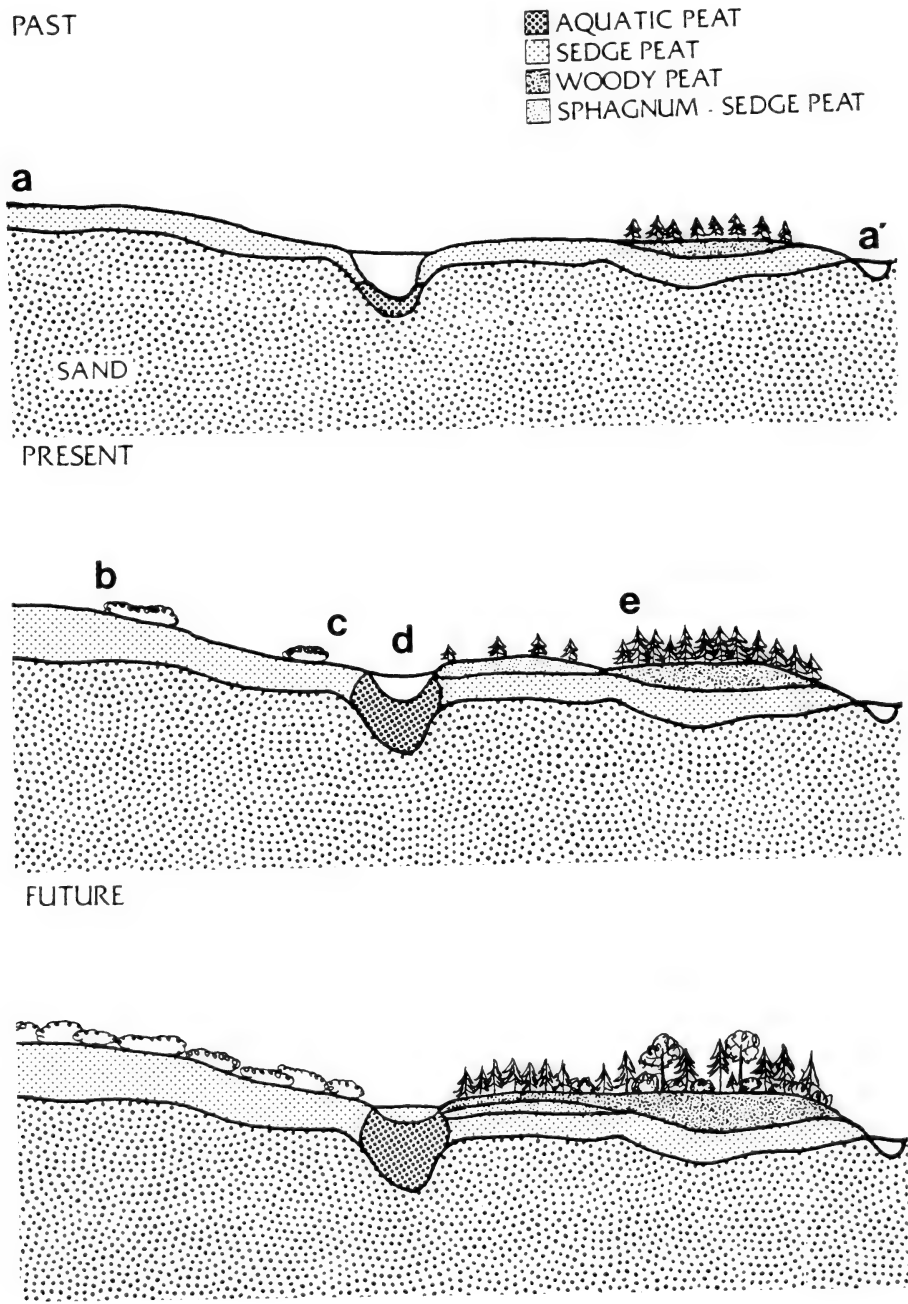


FIG. 3. Peat development in the Hampton Creek wetland along a transect (a-a') through the mesic fen (b), wet fen (c), and emergent aquatic (d) communities and the young tamarack forest (e) studied in Sytsma & Pippen (1982). Vertical scale is exaggerated to show successive peat layers. (Transect location is shown in Fig. 1.)

SUMMARY

Fen succession in the minerotropic and heterogeneous Hampton Creek wetland complex (Kalamazoo County, Michigan) was studied by quadrat and transect vegetational sampling, soil analysis, peat coring, and aerial photo interpretation. Data indicate that the progression from an open aquatic community approximately 11,000 years ago to emergent aquatic, wet fen, mesic fen, shrub-carr, and wet northern forest communities has not followed the orderly sequence or rate usually attributed to such systems. Instead, minute changes in topography, groundwater levels, water chemistry, drainage patterns, and peat accumulation are shown to be important factors in fen succession. Two dominant trends can be seen in the future succession of the peatland complex: first, the invasion by shrub-carr in more mesic fen sites due to artificial drainage of the peat sites and to the absence of fire or mowing; and second, the invasion of the emergent aquatic and wet fen sites by rich stands of Tamarack.

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REVIEW

FLOWERING PLANTS: MAGNOLIAS TO PITCHER PLANTS. The Illustrated Flora of Illinois. By Robert H. Mohlenbrock. Southern Illinois University Press, Carbondale, 1981. 261 pp. \$22.95.

Those who are familiar with Thorne's system of flowering plants, adopted in the present flora, will realize that this volume includes only the "Ranalian" families, both woody and herbaceous (Cronquist's subclass Magnoliidae) plus Sarraceniaceae. Covering 110 species, this installment continues one of the most expensive local floras (on a per species basis) available, which is evidently aimed at generously endowed libraries, specialists interested in only a limited number of families, or perhaps wealthy individuals. It is a reference, not a field manual. The nine volumes (half the flora?) thus far published (three on dicots) already occupy 10 inches of shelf space, with over 70% of the dicot families, plus *Carex*, yet to go. If inflation stops dead (an unreasonable assumption), the entire flora will evidently cost over \$400 for the vascular plants.

The illustrations strike me as excellent, unlike the early volumes and almost as good as those of the previous one, which were the best thus far. As usual, simple keys are included, along with county dot maps (Illinois) for all species, descriptions for all taxa, and additional notes. The format and typography are basically attractive, despite such slips as odd blocks of blank space at the tops of pp. 77, 149, and 197, "left over" from surrounding the maps on the preceding pages. And it is annoying to see in this volume the same strange inconsistency of the previous one in that the names (or abbreviations) of authors of generic names are in italics except for Linnaeus (L.), which is a small capital (except after *Delphinium*). In the first dicot volume (and many of the monocots as well as the ferns) such names were all in small capitals. The sedge volume employed normal roman capitals and lower case consistently for names of all authors.

For botanists with access to it in Illinois and adjacent regions, this flora will doubtless prove useful, although anyone with a critical eye will inevitably wish that the author had done things differently at various points—including not repeating old unreliable statements such as attribution of *Anemone patens* to Michigan. The leaves of *Caltha* are drawn 100% entire, although in Michigan, at least (as stated also by Deam for Indiana), they vary from "almost entire" to (usually) clearly toothed. In *Hepatica americana* (as *H. nobilis* var. *obtusata*), the leaves are drawn much too deeply lobed—in the range for the other taxon. *Anemonella* does not have an "umbel of achenes" as repeatedly stated, but a small umbel of flowers each of which produces several sessile achenes. Fernald's deliberately illegitimate name *Anemone quinquefolia* var. *interior* is used. *Nuphar* is treated as neuter although the name is conserved as feminine. There is no suggestion that *Caulophyllum* consists of two easily distinguished taxa. Attribution of variegated leaf condition in *Argemone* is reversed from Ownbey's cited monograph (and, apparently, nature). Besides the flower and fruit characters stated, the *easiest* way to distinguish *Chelidonium* from *Stylophorum* is that the leaves are alternate. The tubers of *Dicentra cucullaria* are hardly "white," being densely covered with minute pink dots. These are some of the "weeds" this reviewer culled while browsing among the generous harvest of this volume. It is, further, not clear why the first collection or published report referable to Illinois is given for a few species long known from the state, such as *Dicentra cucullaria*, but not for most, including many introduced ones for which this information would be more significant.

—E. G. Voss

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**THE PRESENT STATUS AND FUTURE PROSPECT FOR
THE AMERICAN CHESTNUT IN MICHIGAN.**

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The American chestnut once made up 25 percent of our eastern deciduous forest. Its native range included over 200 million acres (Kuhlman, 1978). It was the fastest growing and most rot-resistant of all our hardwood trees. At its largest (Fig. 1) the chestnut grew to heights of 120 feet with diameters of 7 to 13 feet (Roosevelt, 1902; Jaynes, 1978). Its wood provided everything from telephone poles to fine furniture; its bark produced tannin for tanning leather; the nuts were used as food for wildlife and man.

In 1904 chestnut blight was discovered on trees in parks of the New York Bronx (Merkel, 1905). It was soon determined that the blight was caused by a fungus, *Endothia parasitica*, brought over on Asiatic chestnuts. Presumably the fungus co-evolved with the Asiatic trees and is not harmful to them. However, once established on an American chestnut, it forms large infectious cankers on the bark and quickly destroys the tree (Fig. 2). The blight spread 10 to 15 miles each year, and within 50 years it spread throughout the range of the American chestnut and destroyed 80 percent of the trees (Kuhlman, 1978; USDA, 1954). The blight has been described as the worst ecological disaster in forest history. At present, not a single stand in the native range has remained blight free (Anagnostakis, 1978a).

In 1975 I began study on the former and current range of the American chestnut in Michigan. I knew that the native range of *Castanea dentata* extended only into southeastern Michigan (Saucier, 1973), but early settlers planted the tree beyond its native range, and some of those trees were likely to have remained blight free. The project began by recording locations from specimens at Hope College, Western Michigan University, Michigan State University, University of Michigan, and Cranbrook Institute. The list of chestnuts reported to the Michigan Botanical Club's Big Tree Project was obtained from Paul Thompson. County agents, foresters, and botanists were contacted about locations in specific areas of the state. (James R. Comp, Sr., of Cadillac, was of considerable help in locating trees in the northwestern part of the Lower Peninsula.) The project was mentioned in farmers' news clips, *Michigan Natural Resources*, and broadcasts of two northern radio stations. As reports came in over the last six years, all but ten of the locations (reported by reliable persons) were visited in order to verify the presence of *Castanea dentata*. When there was doubt as to whether a tree was an American chestnut, Graves' key (1961) was used. At each location information was recorded on number of trees, heights and circumferences, condition of blight, if any, and (if possible) when the blight came into the area as recalled by nearby residents. Specimens from each location were

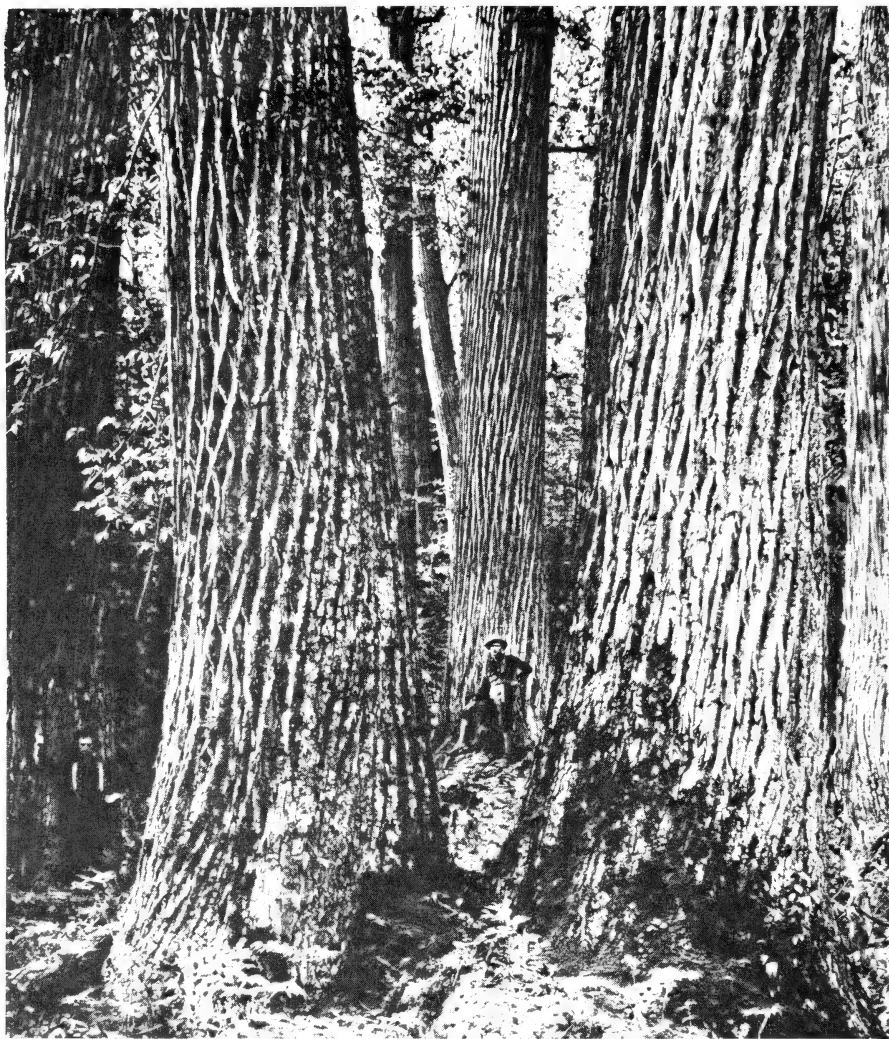


Fig. 1. American chestnuts in the Joyce Kilmer Memorial Forest in North Carolina in 1910 (courtesy Forest History Society, Washington).

placed in the Hanes Herbarium at Western Michigan University. Photographs taken at each site are in the author's possession.

The data from specimens proved to be of little value in locating present-day trees. In most cases the data were not detailed enough or the trees had been removed. However, specimens collected at a number of southeastern locations early in this century were helpful in delineating the native range (Fig. 3). Paul Thompson recently located a large native tree in the Haven Hill recreation area and several blight-free trees near Bloomfield Hills (both localities in Oakland County). However, the American chestnut was never very abundant in its native

range in Michigan. An examination of records for more than 80 townships in southeastern Michigan revealed only five chestnuts serving as witness trees. Thus the tree composed less than one percent of the original forest in Michigan.

Most of the locations visited during the 6-year project were outside the native range. The distribution of many of these chestnuts appears to be correlated with old homesteads and orchards. With the exception of the Manistee National Forest, the fruit belt along the western portion of the Lower Peninsula provided the greatest concentration of trees. Only two locations were reported from the Upper Peninsula (both by Eric Bourdo from the Keweenaw peninsula). Figure 3 shows the number and distribution of trees greater than 6 inches dbh. A total of 224 locations were confirmed; of those 83 showed various stages of disease while 140 were disease-free. Of all the trees with diameters 6 inches or greater, approximately 645 trees were diseased or occurred at diseased sites, whereas 349 chestnuts were found at sites where the blight had not yet entered. Table 1 shows the number of blight-free trees and their diameters.

In order to verify the presence of blight the trees were examined for the yellowish-brown to orange cankers formed by *Endothia*. Only trees with cankers were considered diseased, not those with branches dead because of lightning, winter cold, or other causes. Although the entire tree was examined, more time was spent examining the branches under 8 in. in diameter since the cankers were more obvious on such branches. In nearly all diseased locations at least some of the cankers gave evidence of fruiting bodies (pycnidia or asci).



Fig. 2. An American chestnut hit by blight around 1949, near Kalamazoo. The photo was taken in spring 1981.



Fig. 5. The top photo shows a large blight-free American chestnut in Lake County, while the bottom tree was from a location in Kalkaska Co. The Lake Co. tree has a diameter of 5.5 ft. dbh.

Only 42 blight-free trees exist in the lower half of the Lower Peninsula; no blight-free groves remain. Several locations in the upper part of the Lower Peninsula have 15 or more large blight-free trees. One of the most impressive sites is in Missaukee Co. where there are 27 blight-free trees 10 inches dbh or greater with 2500 naturally produced saplings or small trees 6 inches dbh or less. Figure 4 shows locations where American chestnuts have reproduced naturally. One location in Leelanau Co. has about 1500 blight-free saplings and small trees. If these two populations are not infected in the next 50 years, they should become small chestnut forests. The Benzie County stand described by Thompson had an estimated 3000 naturally produced chestnuts 6 inches dbh or less in 1978 when the blight was thought to have entered.

Why the American chestnut has been able to grow and reproduce so well so far beyond its native range may have resulted from a slow rate of dispersal since glaciation. Davis (1976) pointed out through pollen studies that *Castanea dentata* moved into Michigan less than 1000 years ago and that at the time of the blight the chestnut was still migrating. Studying the dispersal rates at individual locations in northern Michigan might help determine the time it would have taken the species to migrate the length of the Lower Peninsula if no obstacles were encountered. At the Missaukee Co. site mentioned above I observed chestnut saplings up to three-quarters of a mile away from 80-100 year-old trees. The dispersing agents were undoubtedly squirrels and birds.

Since the growing season is long enough for the American chestnut to set seed and reproduce even in the coldest parts of the state, it is not known how far north the tree would have migrated. As a result of the chestnut's ability to grow on a variety of soils (Forest & Cook, 1980), it is likely that it would have found habitats in the north free of competition with northern species. However, the colder parts of the state probably would have been less suitable. A recent examination of locations in the upper part of the Lower Peninsula revealed that the winters of 1977-78 and 1978-79 caused damage to a number of trees. The greatest damage appears to have been away from Lake Michigan in the central and northeastern part of the Lower Peninsula. Jack Kreiner of the Soil Conservation Department in Cadillac has indicated that the greatest damage was done in early December 1977 when the temperature dropped 40° in about 24 hours (USNOAA, 1977). Since the northern limit of the American chestnut in New England and New York was in an area where the average minimum winter temperature is between -20°F and -30°F (USDA, 1960), sudden drops in temperature may be more a cause of winter injury than actual low temperatures.

Tiedemann & Hasselkus (1975) found an American chestnut with no winter injury in Wisconsin where average minimum temperatures range from -30 to -40°F. Before the winter of 1977-78 I did not observe severe cold damage to any Michigan trees. The two locations of American chestnuts in the Upper Peninsula (not visited) have probably been sheltered from extreme cold or great fluctuation in temperature because of their proximity to Lake Superior. In time the American chestnut probably would have migrated northward at least to the middle of the Lower Peninsula and even farther in the western part of the state where winters are less severe and the growing season is longer.

The examination of diseased trees proved to be the most interesting aspect of the study. From the start it was obvious that some trees were more damaged

than others. However, it was not known whether some trees were more resistant or certain strains of the fungus more deadly. In 1977, after reading an article by Van Alfen et al. (1975) and talking with individuals from the Connecticut Agricultural Experimental Station, it became obvious that the situation in Michigan was in some ways similar to that in Europe where the trees have healed naturally.

In Italy the blight infected *Castanea sativa* shortly after it hit *Castanea dentata* in America. However, Biraghi (1951) located some trees in northern Italy that appeared unusually healthy after numerous attacks of the blight. In the 1950's, in France, Grente placed some of the Italian strains on cankers produced by normal virulent strains. The results were that the cankers began to heal and the virulent form of the fungus turned into the non-virulent Italian form. Grente (1965) called these new strains hypovirulent and suggested that genes in the cytoplasm were being transferred from the hypovirulent strains to the virulent ones through anastomosis of hyphae. His theories on hypovirulence were confirmed by Van Alfen et al. (1975). In Italy the chestnut trees have healed naturally, and healing cankers are now prevalent in all the chestnut stands so that the disease is now under control (Mittempergher, 1978). In France, where hypovirulent strains have not had time to develop and spread, Grente has been working on a \$1,500,000 program to inoculate trees with hypovirulent strains (Chelminski, 1979). According to Grente (Hartline, 1980), if 10 cankers are inoculated in one hectare of chestnut orchard, after 10 years the stand can be completely healed.

European hypovirulent strains brought to America have cured individual cankers on *Castanea dentata* (Van Alfen et al., 1975). However, these strains have not spread as in Europe. Unlike the normal virulent strains which produce both ascospores and pycnidiospores, the hypovirulent strains appear to produce only pycnidiospores (Elliston, 1978). The pycnidiospores are forced out in sticky ribbons, probably distributed by birds and insects. Some vegetative mycelium may be dispersed this way as well. It is not known whether vectors capable of dispersing the hypovirulent strains exist in America.

The first American record of hypovirulence came from a grove near Rockford, Michigan, in 1976 when Priscilla Johnson sent bark samples to the Connecticut Agricultural Experimental Station. The fungus proved to have the double-stranded RNA of hypovirulent strains and was able to cure individual cankers (Anagnostakis, 1978a). Hypovirulent strains have also been confirmed from a site near Grand Haven, Michigan, and localities in Tennessee and Virginia (Hartline, 1980). The Grand Haven location was reported to this project in 1975 by Mary Reinoldt. Hypovirulence was confirmed from the site in 1978 by Peter Day of the Connecticut Agricultural Experimental Station. According to George Unger, who has lived on the Grand Haven site more than 70 years, the blight entered the site about 1945 at which time the trees began to die rapidly. However, after about 10 to 15 years the death rate slowed down so that new growth began to equal the amount of dying back. In recent years only small branches have died back (Fig. 6). Cores taken from a number of larger trees show that most trees have maintained slow growth in the last 30 years, with one tree showing a dramatic increase in growth (Brewer, 1979). The smaller 25- to 35-year old trees which never suffered damage from the virulent strains have maintained a rapid growth of about one-half inch in diameter per year. (Because of



Fig. 6. Mary Reinoldt reported the American chestnuts in the top photo near Grand Haven in 1975; these trees have had the blight for over 35 years and possess hypovirulent strains of *Endothia parasitica*. Richard Pippen reported the bottom tree near Bangor in 1975; this tree had had the blight for over 25 years. Both photos were taken in summer 1980.

its potential value to science, this Grand Haven site is being purchased by the Michigan Nature Conservancy.)

Although only the Grand Haven and Rockford sites have confirmed hypovirulence, I have observed significant numbers of healing cankers at 24 southwestern Michigan localities and five in the northwest (Fig. 3). Virulent cankers are nearly always flush with the bark, are seldom swollen, and do not have noticeable healing tissue. Non-virulent cankers which persist for many years are nearly always swollen and show signs of continuous growth (Fig. 7).

The important fact about the Michigan trees is that in certain groves healing cankers have spread throughout the population and the trees have survived in spite of blight. The ability of trees with these cankers to survive for extended periods is evident from the dates in which the blight first entered, the present stem sizes, and tree cores taken at specific sites. To what extent hypovirulent strains suppress virulent strains in Michigan is not known. The fact that hypovirulent strains are not spread by wind-dispersed ascospores makes it hard to believe that they are capable of keeping the virulent strains in check. However, as Mittenpergher (1978) pointed out, a possible explanation for the spread of hypovirulent strains is that they may be more adaptable in the saprophytic phase than virulent strains. If this is so, we may have areas in Michigan saturated



Fig. 7. The photo on the left, taken in Allegan Co., shows a typical deadly canker. The photo on the right was taken from Grand Haven location and shows a canker with healing tissue.

with hypovirulent strains with very few virulent strains remaining. Also, Michigan's environment may be more favorable than other states' for hypovirulent strains. Consequently, further research should determine the environmental factors important for survival of hypovirulent and virulent strains.

Understanding how hypovirulent strains have been dispersed in Michigan may have significance in determining whether the strains can be used in biological control. A preliminary study (Brewer, 1979) indicates that the parts of the tree most visited by certain birds have survived the best. The question of whether hypovirulent strains are being dispersed between groves miles apart or have arisen at various locations should be answered.

In addition to the dispersal problem, recent evidence indicates that certain hypovirulent strains are incompatible with certain virulent strains (Anagnostakis, 1977, 1978b; MacDonald & Double, 1979). If too many incompatible strains are found in a given area, the use of hypovirulence as a biological control device may be complicated. One solution may be to use a mixture of hypovirulent strains to control the blight (Hartline, 1980).

Hybrids between American and Chinese chestnuts have not been considered sufficiently resistant to replace the American chestnut in our eastern deciduous forest. However, if hypovirulence can control the blight, hybrids with good forest characteristics and slightly more resistance might have considerable value. One location in Calhoun Co. has 16 hybrids between American and Chinese trees over 50 ft. high. Within the last two years blight has entered the location, and there are signs of cankers similar to those at proven hypovirulent locations. These trees should be closely observed.

SUMMARY AND CONCLUSION

A total of 224 locations of American chestnuts were examined in Michigan between 1975 and 1981, 84 in various stages of disease and 140 disease-free. Of all the trees 6 inches dbh or greater, approximately 645 were diseased or occurred at diseased sites, whereas 349 were found at sites free of blight. Damage ranged from death after 3 or 4 years to survival of over 45 years with healing cankers. Twenty-four locations in southwestern Michigan and five in the northwest had significant amounts of healing cankers. The ability of trees with these cankers to survive the blight for extended periods of time was evident from the dates in which the blight first entered, the present stem sizes, and tree cores taken at specific sites.

Although the American chestnut is close to extinction in its Michigan native range, blight-free trees survive in numerous locations outside the native range. How long these trees will remain isolated from blight will probably depend on the ability of the fungus to disperse and live on various substrates. More research should be done to determine what other tree species provide host material for *Endothia parasitica*. In five Michigan locations where diseased trees were completely removed, blight-free chestnuts have been planted and have continued to be blight-free. This fact may be encouraging to owners of blight-free trees which are isolated from diseased trees. Eventually most of these trees will probably become infected, but for the time being Michigan has more than its share of mature American chestnuts.

In addition to the large surviving American chestnuts and the naturally produced smaller trees, a large number of seedlings are being introduced around the state. In the last three years over 150,000 American chestnut seeds collected by James R. Comp, Sr., and others in the Cadillac area have been planted by the Soil Conservation Department, and seedlings are being distributed throughout the state. Although these new trees may provide new host material for the blight, they will probably assure the existence of at least some

blight-free trees. Ultimately, however, survival will probably depend on how well hypovirulent strains can control the blight and to what degree man can aid nature in bringing back the chestnut.

I am indebted to the late Dr. William T. Gillis for his work on this project and dedicate this paper to him. He was instrumental in getting the project started and spent considerable time sending out many of the early letters. His enthusiasm for botany and concern for his students greatly stimulated my own interest. I am also indebted to James R. Comp, Sr., who spent many hours helping to track down trees on back roads in the northern Lower Peninsula. Paul Thompson and the Michigan Botanical Club supplied a large number of locations. Richard Arps and Bernard Hubbard also compiled long lists of chestnuts. Dr. Richard Brewer, Dr. Richard Pippen, Gordon Brewer, and Kim Chapman read the manuscript and made helpful comments. I am also thankful for more than 100 individuals who sent locations of chestnuts.

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MICHIGAN PLANTS IN PRINT

(U. S. Geological Survey). The new topographic maps for Michigan listed below have been published since the previous listing in our October 1978 issue and are available at \$2.00 each from Eastern Distribution Branch, U. S. Geological Survey, 1200 South Eads St., Arlington, Virginia 22202. The Garden Island West quadrangle completes initial coverage of the state (contrary to earlier claims of final coverage!). Other maps listed are at a larger scale than older 15-minute maps including the same areas. These are all 7½-minute quadrangles (scale of 1:24,000 or about 2½ inches to a mile, with a basic 10-foot contour interval, except for those quadrangles marked with an asterisk (*), which are at a scale of 1:25,000 with a contour interval of 5 meters); worthy as conversion to the metric system may be, it is unfortunate that adjacent maps, surveyed and published in identical years and formerly parts of the same 15-minute quadrangle, are not available at the same scale or with the same contour interval. Quadrangles marked ** are metric, for areas 7.5 × 15 minutes. To save space, photorevised maps, the new land use and land cover maps, and orthophotoquads are not listed here. One county topographic map has been published for Michigan, for St. Clair County, scale of 1:100,000, contour interval 10 meters, price \$3.25 from same address. Following the name of each quadrangle below, the county or counties in which it primarily lies are indicated in brackets.

Aldridge Creek* [Ontonagon]
 Alto [Kent]
 Black River Harbor** [Gogebic]
 Carp River** [Ontonagon]
 Cascade [Kent]
 Casnovia [Ottawa, Muskegon, Kent]
 Charlotte [Eaton]
 Chester [Eaton]
 Coopersville [Ottawa]
 Duck Lake [Eaton, Calhoun]
 Eagle [Clinton]
 Freeport [Kent, Ionia]
 Garden Island West [Charlevoix]
 Hoytville [Eaton]
 Hudsonville East [Allegan]
 Hudsonville West [Allegan]
 Ionia [Ionia]
 Lake Odessa [Ionia]
 Litchfield [Calhoun, Hillsdale]
 Little Girls Pt. [Gogebic + Wis.]
 Lowell [Ionia, Kent]
 Lyon Lake [Calhoun]
 Manchester [Washtenaw]
 Marne [Ottawa, Kent]
 Marshall [Calhoun]

Mosherville [Hillsdale, Jackson]
 Nashville [Eaton, Barry]
 Needmore [Eaton]
 North Ironwood** [Gogebic]
 Northwest Albion [Calhoun]
 Norvell [Jackson]
 Olivet [Eaton, Calhoun]
 Oronto Bay [Gogebic + Wis.]
 Parma [Jackson]
 Portland North [Ionia]
 Portland South [Ionia]
 Ravenna [Muskegon]
 Saranac [Ionia]
 Saubee Lake [Eaton, Barry]
 Southeast Albion [Jackson]
 Southwest Albion [Calhoun]
 Spring Arbor [Jackson]
 Springport [Eaton, Jackson]
 Tekonsha [Branch, Calhoun]
 Thomaston** [Gogebic]
 Tiebel Creek** [Ontonagon]
 Tipton [Washtenaw, Lenawee]
 Westphalia [Clinton]
 Woodbury [Ionia]
 Woodland [Barry]

B. BOOKS, BULLETINS, SEPARATE PUBLICATIONS

- Barnes, Burton V., & Warren H. Wagner, Jr. 1981. Michigan Trees. Revised and Enlarged Edition of Charles Herbert Otis's Michigan Trees. Univ. Mich. Press, Ann Arbor. 384 pp. \$5.95 (paper); \$10.95 (cloth). [A long-awaited work, reviewed in Mich. Bot. 21: 46.]
- Brodo, Irwin M., & David L. Hawksworth. 1977. Alectoria and Allied Genera in North America. Op. Bot. 42. 164 pp. [*Bryoria chalybeiformis*, *B. fuscescens*, *B. trichodes*, *B. furcellata*, *B. capillaris*, and *B. nadvornikiana* are mapped at Michigan localities and selected specimens are cited of these lichens.]
- Given, David R., & James H. Soper. 1981. The Arctic-Alpine Element of the Vascular Flora at Lake Superior. Natl. Mus. Canada Publ. Bot. 10. 70 pp. [Michigan localities are included in the distribution maps; see review in Mich. Bot. 21: 65.]
- Kärnefelt, Ingvar. 1979. The Brown Fruticose Species of *Cetraria*. Op. Bot. 46. 150 pp. [*C. arenaria*, *C. ericetorum* ssp. *reticulata*, and *C. islandica* ssp. *crispiformis* cited and mapped from Michigan localities.]
- Little, Elbert L., Jr. 1977. Atlas of United States Trees Vol. 4. Minor Eastern Hardwoods. U. S. Dep. Agr. Misc. Publ. 1342. 17 pp. + 230 maps. \$8.75. [The distribution maps for these "minor" trees—often large shrubs—usually include Michigan when appropriate, but not always accurately; see notice in Mich. Bot. 19: 46.]
- Loomis, Robert M., & Richard W. Blank. 1981. Summer Moisture Content of Some Northern Lower Michigan Understory Plants. U. S. Dep. Agr. For. Serv. Res. Note NC-263. 4 pp. [Average seasonal moisture contents were determined on several common plants of jack pine-oak areas in Roscommon Co. in order to estimate fire behavior trends. Data are given for the full season (June 13-Sept. 6) and for each half of it for *Maianthemum*, *Aster macrophyllus*, *Pteridium*, *Comptonia*, *Rubus* spp., *Vaccinium* spp., *Carex* spp., and mixed grasses.]
- McNabb, Clarence D., Jr. 1977. Aquatic Plant Problems in Recreational Lakes of Southern Michigan. Mich. St. Univ. Ext. Bull. E-1135. 25 pp. \$2.00. [See notice in Mich. Bot. 19: 74.]
- Ohmann, L. F., et al. 1978. Some Harvest Options and their Consequences for the Aspen, Birch, and Associated Conifer Forest Types of the Lake States. U. S. Dep. Agr. For. Serv. Gen. Tech. Rep. NC-48. 34 pp. [Includes map of distribution of the aspen-birch, spruce-fir, and white-red-jack pine forest types in Michigan, Minnesota, and Wisconsin.]
- Priwer, Hannah, George Ayers, John Stuurwold, & Alan R. Putnam. 1980. Guide to the Identification of Common Weed Seedlings of Michigan. Mich. St. Univ. Ext. Bull. E-1363. 8 pp. \$.65. [Includes no general comments or introduction at all, but consists of a "key" and excellent color photos of seedlings with brief descriptions; also tiny color photos of mature plants ("*Polygonum pensylvanicum*" is clearly not that) and, for biennials and perennials, spring rosettes or sprouts. A useful guide—if one knows he has one of the 28 species included.]
- Rice, Robert P., Jr., Alan R. Putnam, & Ronald H. Lockerman. 1976. Problem Perennial Weeds of Michigan. Mich. St. Univ. Ext. Bull. E-791. 20 pp. \$1.00. [Guide to 42 weeds; see notice in Mich. Bot. 19: 90.]
- Smith, Alexander H., Helen V. Smith, & Nancy S. Weber. 1979. How to Know the Gilled Mushrooms. Wm. C. Brown, Dubuque. 335 pp. \$6.95 (wire); \$8.95 (cloth). [Many species are said to grow in the Great Lakes region and a very few explicitly in Michigan; see notice in Mich. Bot. 19: 74.]
- Swink, Floyd, & Gerould Wilhelm. 1979. Plants of the Chicago Region. Rev. & Exp. Ed. Morton Arb., Lisle, Ill. lxxiii + 922 pp. \$14.00. [This 3rd edition adds keys and much new information, including additional species from Berrien Co.; see review in Mich. Bot. 19: 36.]
- Willis, Gary L., & James A. Johnson. 1978. Regeneration of Yellow Birch Following Selective Cutting of Old-Growth Northern Hardwoods. Mich. Tech. Univ. Ford For. Center Res. Notes 26. 13 pp. [Growth of yellow birch in relation to environmental conditions in Marquette Co.]
- Winsauer, Sharon A., & Helmuth M. Steinhilb. 1981 ["1980"]. Summary of Green Weights and Volumes for Five Tree Species in Michigan. U. S. Dep. Agr. For. Serv. Res. Pap.

NC-191. 22 pp. [Summarizes data from western Upper Peninsula presented in three previous papers (not listed here), with tables and graphs for weight and volume of total tree, bole, and residue for aspen, white spruce, red pine, balsam fir, and sugar maple.]

C. JOURNAL ARTICLES

- Ahern, Phyllis J., & Robert E. Bailey. 1980. Pollen record from Chippewa Bog, Lapeer County, Michigan. *Mich. Academ.* 12: 297–308. [Includes particular observations on arrival of beech in Michigan; corrections noted on p. 388 in next issue of same journal.]
- Aiken, S. G., P. R. Newroth, & I. Wile. 1979. The biology of Canadian weeds. 34. *Myriophyllum spicatum* L. *Canad. Jour. Pl. Sci.* 59: 201–215. [Includes statement that this weed has “spread to every county in Southern Michigan” but there is no definition of “Southern” nor statement as to specimen documentation for this assertion.]
- Ambrose, J. D. 1980. A re-evaluation of the Melanthioideae (Liliaceae) using numerical analyses. *Linn. Soc. Symp. Ser. 8* (Petaloid Monocotyledons): 65–82. [Among the material examined was *Tofieldia glutinosa* from Snyder Lake [Washtenaw Co.], Michigan.]
- Andrus, Richard E. 1980. *Sphagnum subtile* (Russow) Warnst. and allied species in North America. *Syst. Bot.* 4: 351–362. [Citations of selected specimens of *S. subtile* include three northern Michigan counties, and four appear to be shown on distribution map; generalized maps include Michigan in range of two related species.]
- Bailey, Robert E., & Jack E. Chaney. 1980. Diversity patterns and community structure of an old field in Veit’s woodlot, Central Michigan University. *Mich. Academ.* 12: 497–515. [Vegetation study at the edge of Mount Pleasant.]
- Barkley, T. M. 1978. *Senecio*. *N. Am. Fl. II*, 10: 50–139. [Michigan mentioned in the range of *S. plattensis* but not for our other species, for which this monograph does not include detailed distributions or illustrations; however, there are useful synonymy, descriptions, and keys. See notice in *Mich. Bot.* 20: 188.]
- Baskin, Jerry M., & Carol C. Baskin. 1977. Dormancy and germination in seeds of common ragweed with reference to Beal’s buried seed experiment. *Am. Jour. Bot.* 64: 1174–1176. [Comments on season of germination tests and possible dormancy as affecting results of Beal’s noted long-term experiment at M.S.U.]
- Bigelow, Howard E. 1976. Studies on some lignicolous Clitocybes. *Mem. N. Y. Bot. Gard.* 28: 9–15. [Includes description of *C. americana* with type locality Colonial Point, Burt Lake, Cheboygan Co.]
- Brouillet, Luc, & Jean-Pierre Simon. 1981. An ecogeographical analysis of the distribution of *Aster acuminatus* Michaux and *A. nemoralis* Aiton (Asteraceae: Astereae). *Rhodora* 83: 521–550. [Distribution map shows westernmost localities for *A. nemoralis* in eastern Upper Peninsula.]
- Bruce, James G., & Joseph M. Beitel. 1979. A community of *Lycopodium* gametophytes in Michigan. *Am. Fern Jour.* 69: 33–41. [Report, with key and illustrations, on nearly 500 gametophytes of at least five species discovered in a jack pine plantation in Mecosta Co.]
- Bruce, James G. 1979. Gametophyte of *Lycopodium digitatum*. *Am. Jour. Bot.* 66: 1138–1150. [Thorough study, based on material (only indirectly cited) from Mecosta Co.]
- Buech, Richard R. 1980. Vegetation of a Kirtland’s Warbler breeding area and 10 nest sites. *Jack-Pine Warbler* 58: 59–72. [General data from Oscoda and Crawford Cos.]
- Butterfield, Ira W. 1979. The Jahr site (20 TU 6) Tuscola County, Michigan. *Mich. Archaeol.* 25: 75–134. [Includes a list, with numerous errors in transcription, of almost 50 vascular plant species at the archeological site before it was destroyed.]
- Cecich, Robert A. 1977. An electron microscopic evaluation of cytohistological zonation in the shoot apical meristem of *Pinus banksiana*. *Am. Jour. Bot.* 64: 1263–1271. [Seeds used in the study were from the Upper Peninsula.]
- Coffey, Vincent J., & Samuel B. Jones, Jr. 1980. Biosystematics of *Lysimachia* section *Seleucia* (Primulaceae). *Brittonia* 32: 309–322. [Maps—with remarkably evenly spaced dots—show distribution of *L. ciliata*, *L. lanceolata*, and *L. quadriflora* in Michigan; the author annotated a Michigan specimen of *L. hybrida* in 1973 but it is not mapped. Includes key, descriptions, and synonymy, but no citations of specimens.]

IDENTIFICATION OF THE SPECIES OF *CAREX* IN MICHIGAN'S UPLAND DECIDUOUS FORESTS: A KEY STRESSING VEGETATIVE FEATURES

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For much of the year, accurate identification of many species of *Carex* is impossible without the assistance of an expert botanist or the resources of a large herbarium. Most of the available floras have keys emphasizing characters of achene, perigynium, or spikelet. If a specimen has no ripe achenes (if it is in flower or if all the fruits have fallen off), then identification becomes difficult.

This key is designed to aid botanists and ecologists by extending the period of time in which specimens of *Carex* from Michigan's upland deciduous forests can be collected and accurately identified: specimens which have an elongated fertile culm in any stage of maturity should be identifiable using this key.

By presenting a key stressing vegetative features I do not wish to imply that the more obscure features of achene or perigynium are to be dismissed as unimportant. These technical characters are extremely valuable because they are, compared to vegetative features, constant within each species. Vegetative features may be strongly influenced by their environment, and therefore often have wide ranges of variability. As a result, this key sacrifices some reliability in order to extend the period during which species can be collected and identified.

Upland deciduous forests are an important part of Michigan's vegetation and are composed primarily of oak-hickory and beech-maple associations although birch, basswood, and aspen may be of importance. In constructing this key, it was necessary to omit the sedges of lowland deciduous forests (floodplains, swamp forests, and moist depressions in upland forests). Not only would this have required including species typical of floodplain and swamp forests, but, as many marsh and bog species are occasionally found in these wet forests, those sedges would have had to be included as well. The number of species would have become unmanageable. However, a number of species characteristic of wet forests also occasionally occur in upland forests and have therefore been included. Consequently, many of the plants growing in depressions in upland deciduous forests should key out successfully. Unfortunately, this will not always be the case, because the swamp forest species included here are only those most likely to occur on drier sites.

When collecting material to be identified using this key, it is crucial to collect all parts of the plant including the roots or rhizomes. Since certain important identifying characters (the achenes and perigynia) are not used in this key, the necessity of collecting other parts of the plant becomes much greater. The collector should choose plants typical of the population and as close to maturity as possible and should beware of adventives: occasionally plants normally

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occurring in very different habitats will, by chance, become established in the deciduous forest. These plants usually grow poorly and are present in small numbers.

To use this key properly, certain morphological terms peculiar to sedges, particularly those describing the leaves, must be understood. The leaves can be divided into two distinct parts: the blade and the sheath. The blade is the long, flattened distal portion (Fig. 1a, b). The sheath is the short basal portion which completely surrounds the stem or culm; it is fused around the culm or stem forming a tube. The membranous side of the sheath opposite the blade is called the inner band (Fig. 1a, b). Opposite the summit of the inner band is the junction between blade and sheath. The line at this junction, the ligule, is a long flap of tissue in the shape of an inverted "V" (Fig. 1b). At the base of the plant may be one to several leaves with blades highly reduced; these are called bladeless sheaths (Fig. 1c). Basal leaves arise at or very near the base of the plant; cauline or culm leaves arise from the fertile or flowering culm (Fig. 1c).

1. Basal leaves, sheaths, bladeless sheaths, at least in part, red, maroon, purple, or streaked with those colors.
 2. Leaves over 10 mm (rarely 8 mm) wide, with 3 to 5 prominent veins, usually less than 30 cm long, evergreen; culms slender, naked.
 3. Leaves mostly 2–3 cm wide; bladeless sheaths and base of some leaf blades red.
 1. *C. plantaginea*
 3. Leaves mostly 0.8–2 cm wide; only lowest sheaths red.
 2. *C. careyana*
 2. Leaves mostly less than 10 mm wide, with or without prominent veins, more or less than 30 cm long, evergreen or not; culms various.
 4. Leaves, at least some portion (excluding area directly above the ligule) pubescent, the hairs easily visible with a hand lens.
 5. Leaf pubescence restricted to sheaths, the hairs short and sparse.
 3. *C. gynandra*
 5. Leaf pubescence not restricted to sheaths, the hairs various.
 6. Leaf blade equally pubescent on both sides.
 7. Larger basal leaves less than 3.5 mm wide, grayish-green, usually less than 30 cm long.
 4. *C. hirsutella*
 7. Larger basal leaves more than 3.5 mm wide, grayish-green or not, usually more than 30 cm long.
 5. *C. hirtifolia*
 6. Leaf blade much more pubescent on abaxial side than on adaxial side (abaxial side long pubescent on distal 25%, adaxial pubescence, if any, shorter and appressed).
 8. Inner band of leaf sheath glabrous [the next 2 species are closely related and difficult to distinguish vegetatively].
 9. Pistillate scales of spikelets acute, not awned.
 6. *C. formosa*
 9. Pistillate scales of spikelets awned.
 7. *C. davisii*
 8. Inner band of leaf sheath pubescent.
 10. Ligule not fringed with hairs, its tip rounded.
 8. *C. swanii*
 10. Ligule fringed with hairs, its tip acute.
 9. *C. virescens*
 4. Leaves glabrous, or pubescent only directly above ligule.
 11. Fertile culm flattened at summit, almost filiform near base; inflorescence bracts leaflike, 1–5.5 cm long; leaves exceeding inflorescences.
 12. Leaves 2–3 mm wide; only in the southern Lower Peninsula.
 10. *C. jamesii*
 12. Leaves 4–5.5 mm wide; only in the Upper Peninsula and the northern Lower Peninsula.
 11. *C. backii*
 11. Culm not flattened at summit or not filiform at base or inflorescence bracts not leaflike or leaves not exceeding inflorescences.

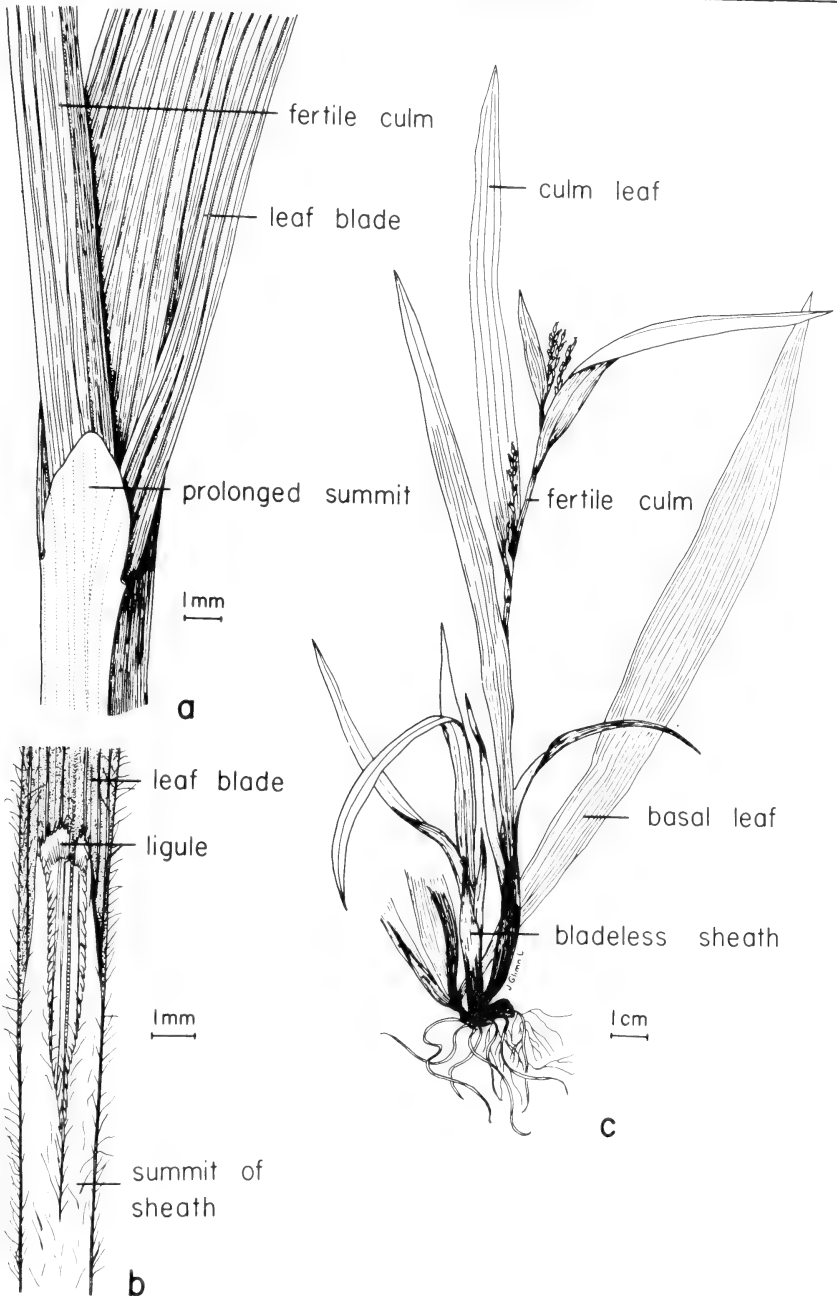


Fig. 1. Vegetative characters of *Carex*. a. *C. granularis*: base of cauline leaf blade, fertile culm, and summit of inner band of leaf sheath. b. *C. castanea*: base of leaf blade, fringed free portion of ligule, and summit of inner band of leaf sheath. c. *C. albursina*: habit showing basal bladeless leaf sheaths, basal leaves, cauline or culm leaves, and fertile culm with inflorescence.

13. Leaf sheaths with raised septa between the veins; bracts subtending the inflorescence many times longer than inflorescence. 12. *C. retrorsa*
13. Leaf sheaths without raised septa between the veins or bracts subtending inflorescence not many times longer than inflorescence.
14. Summit of inner band of lower cauline leaves prolonged, with or without a notch, clearly not concave.
15. Summit of inner band notched; Upper Peninsula and northern Lower Peninsula. 13. *C. ormostachya*
15. Summit of inner band without a notch.
16. Leaves over 3.5 mm wide; fruiting culm over 40 cm tall.
17. Inner band of lower leaves whitish-hyaline; southern Lower Peninsula. 14. *C. gracilescens*
17. Inner band of lower leaves brownish to reddish; throughout the state. 15. *C. gracillima*
16. Leaves up to 3 mm wide; fruiting culm up to 25 cm tall; southernmost counties. 16. *C. oligocarpa*
14. Summit of inner band of lower cauline leaves concave to truncate.
18. Leaves up to 2.5 mm (rarely to 3.0 mm) wide. [Four species of the Montanæ group key out here. Their vegetative characters seem to intergrade completely. The key for these species shows only tendencies. For accurate identification, fruiting material is essential.]
19. Summit of inner band of leaf sheath almost truncate, slightly concave; plants not densely cespitose; Upper Peninsula and northern Lower Peninsula. 17. *C. peckii*
19. Summit of inner band distinctly concave; plants densely cespitose to rhizomatous.
20. Adaxial surface of leaf blade above ligule usually pubescent; plants densely cespitose, not rhizomatous; southern Lower Peninsula. 18. *C. emmonsii*
20. Adaxial surface of leaf blade above ligule glabrous to puberulent; plants rhizomatous or not.
21. Summit of inner band deeply concave, often without a pubescent fringe; rhizomes and leaf bases with only a slight red tinge at most; plants clumped, with long rhizomes; throughout Michigan. 19. *C. pensylvanica*
21. Summit of inner band concave to almost truncate, usually with a pubescent fringe; leaf bases always tinged with red; densely cespitose; plants not rhizomatous; southwestern Lower Peninsula. 20. *C. artitecta*
18. Most leaves over 3 mm wide.
22. Free portion of the ligule yellow-brown, brown, or reddish, distinctly darker than nearby portions of the leaf or sheath.
23. Outline formed by the free portion of the ligule usually longer than wide; some leaves overwintering.
24. Sheath red-dotted ventrally. 21. *C. debilis*
24. Sheath not red-dotted ventrally. 22. *C. communis*
23. Outline formed by the free portion of the ligule usually shorter than wide to as long as wide; leaves overwintering or not.
25. Culms less than 0.7 mm wide at 5 cm from base; plants less than 0.3 m tall. 23. *C. pedunculata*
25. Culms over 1 mm wide at 5 cm from the base; plants 0.3 m to 1 m tall.
26. Summit of inner band of culm leaves below the inflorescence prolonged and usually light.
27. Plants densely cespitose, without elongate horizontal rhizomes; leaves less than 6(8) mm wide. 24. *C. intumescens*

27. Plants caespitose or with solitary culms, with elongate horizontal rhizomes; leaves usually over 6(4) mm wide. 25. *C. lupulina*
26. Summit of inner band of culm leaves below the inflorescence concave and darkened, brownish. 26. *C. grayii*
22. Free portion of ligule hyaline for its entire length, whitish, yellowish, or greenish; not conspicuously darker than nearby portions of leaf or sheath.
28. Largest basal leaves 5.5–10 mm wide.
29. Base of lowest green leaf blade 10–20 cm above base of plant. 27. *C. crinita*
29. Base of lowest green leaf blade 1–5 cm above base of plant. 28. *C. arctata*
28. Largest basal leaves 2–5.5 mm wide.
30. Plant without scaly rhizomes but from a stout, semi-woody rootstock; some leaves overwintering; all sheaths red. 23. *C. pedunculata*
30. Plant with scaly rhizomes or loosely caespitose, not from a stout rootstock; no leaves overwintering; sheaths red or not.
31. Plant markedly red at base, the red often extending several cm up leaf sheaths; plants with scaly rhizomes or stolons up to 10 cm long. 29. *C. woodii*
31. Plant with only a little red at base, the color limited to several basal bladeless sheaths which are dark-maroon; plants loosely caespitose or with rhizomes up to 3 cm long. 30. *C. prasina*
1. Basal leaves, sheaths and bladeless sheaths yellow to brown, without any red, mahogany, or purple at base.
32. Sterile shoots numerous, the fertile shoots few in comparison; leaves of sterile shoots conspicuously 3-ranked and \pm crowded; southern Lower Peninsula. 31. *C. muskingumensis*
32. Sterile shoots few or absent or leaves of sterile shoots not conspicuously 3-ranked; throughout.
33. Mature leaves over 13 mm wide *and* less than 15 cm long; culm leaves much smaller than basal leaves, usually less than 7 mm wide; St. Clair and Berrien counties. 32. *C. platyphylla*
33. Mature leaves less than 13 mm wide, *or* more than 15 cm long, *or* culm leaves nearly as wide as basal leaves, usually over 10 mm wide.
34. Culm flattened at summit, almost filiform near base; inflorescence bracts leaflike, 1–5.5 cm long; leaves exceeding inflorescences.
35. Leaves 2–3 mm wide; southern Lower Peninsula. 10. *C. jamesii*
35. Leaves 4–5.5 mm wide; Upper Peninsula and northern Lower Peninsula. 11. *C. backii*
34. Culm not flattened at summit or not filiform at base or inflorescence bracts not leaflike or leaves not exceeding inflorescence.
36. Culm sharply angled, with concave sides, almost winged; inner band usually puckered; inflorescence \pm congested; leaves 4–8 mm wide. 33. *C. stipata*
36. Culm not sharply angled or inner band not puckered; inflorescence and leaves various.
37. Leaf sheaths with raised septa between veins; bract subtending inflorescence leaflike and many times longer than the inflorescence. 12. *C. retrorsa*
37. Leaf sheaths without raised septa between veins; bracts subtending the inflorescence various.
38. Summit of inner band of lower cauline leaf sheaths prolonged or convex (it may appear somewhat "V" shaped with 1 side prolonged).
39. Inner band hispidulous and tinged brownish toward the apex. 34. *C. hitchcockiana*

39. Inner band glabrous at apex or not tinged brownish.
 40. Basal leaf sheaths whitish to greenish-white or yellowish; fertile culms erect.
 35. *C. amphibola*
40. Basal leaf sheaths yellowish to brownish; fertile culms lax.
 41. Basal leaves at least partially evergreen; terminal spikelet staminate.
 14. *C. gracilescens*
41. Basal leaves not evergreen; terminal spikelet mostly pistillate.
 36. *C. projecta*
38. Summit of inner band of lower cauline leaf sheaths concave to truncate or "V" shaped, never prolonged.
42. Mature leaves mostly less than 3.2 mm wide. [Several species are identifiable through both leads of this couplet.]
43. Adaxial surface of leaf above free portion of ligule minutely pubescent.
 29. *C. woodii*
43. Adaxial surface of leaf glabrous above ligule.
44. Leaves mostly 1–2 mm wide; bract subtending lowest spikelet oblong, hyaline, with a green nerve, not filiform; summit of inner band often slightly thickened.
 37. *C. bromoides*
44. Leaves mostly 2–3.2 mm wide; bract subtending lowest spikelet filiform for most of length; summit of inner band seldom thickened. [*C. rosea* and *C. convoluta* are often lumped under *C. rosea* and are frequently inseparable on vegetative characters.]
45. Wider leaf blades mostly 0.9–1.9 mm broad.
46. Culms scabrous above; spikelets with male flowers at base.
 38. *C. brunnescens*
46. Culms not scabrous above; spikelets with male flowers at apex.
 39. *C. rosea*
45. Wider leaf blades 1.7–3.2 mm wide.
47. Inflorescence interrupted, the spikelets peduncled or at least separated from each other.
48. Spikelets roughly spherical; free portion of ligule 0.1–0.2 mm long.
 40. *C. convoluta*
48. Spikelets obovoid or cylindrical; free portion of ligule 0.3–1 mm long.
49. Leaves \pm basal or with base of leaf blades within 5 cm of base of plant; spikelets obovoid.
 41. *C. deweyana*
49. Leaves cauline, with bases of leaf blades mostly 5 cm or more from base of plant (excluding sheaths with shortened blades); spikelets obovoid or spherical.
50. Leaves 1.4–2.5 (3.5) mm wide; most frequent in the southern Lower Peninsula.
 42. *C. tenera*
50. Leaves 2–3.2 (4) mm wide; throughout the state. [This keys out 2 very similar species which are often not separable by non-technical characters.]
51. Spikelets greenish-yellow or brownish; perigynia nerveless.
 43. *C. aenea*
51. Spikelets silvery-green to pale brown; perigynia nerved on ventral face.
 44. *C. argyrantha*
47. Inflorescence not interrupted, \pm ovoid, the spikelets crowded.
52. Plant densely caespitose, the bases only slightly fibrous, if at all.
 45. *C. cephalophora*
52. Plant stoutly rhizomatous, the bases fibrous.
 46. *C. muhlenbergii*
42. Mature leaves mostly more than 3.5 mm broad.
53. Plants with thickly fibrous bases due to partial decomposition of old leaves.
 47. *C. spengelii*
53. Plants without thickly fibrous rhizomes various or absent.

54. Leaf doubly folded, "M" shaped in cross section; the midvein and two midlateral veins distinct for most of the leaf length.
55. Leaves scabrous; rhizomes horizontal; culms sharp-angled and scabrous. 48. *C. scabrata*
55. Leaves not scabrous or plant without horizontal rhizomes or culms not sharp-angled and scabrous.
56. Culms sharp-angled and lightly scabrous; plant caespitose; larger leaves mostly 3.5–4 mm wide. 30. *C. prasina*
56. Culms not sharp-angled; plant caespitose or not; leaves various.
57. Larger leaves mostly 3.5–5 mm wide.
58. Inner band often cinnamon-tinged and red-dotted; inflorescence usually not exceeding basal leaves; southern Lower Peninsula. 49. *C. digitalis*
58. Inner band whitish to cinnamon-tinged, not red-dotted; inflorescence usually exceeding basal leaves; Upper Peninsula and northern Lower Peninsula. 13. *C. ormostachya*
57. Larger leaves mostly over 5 mm wide.
59. Leaves mostly 9–13 mm wide, less than 15 cm long; inner band usually red-dotted; angles of culm not winged; St. Clair and Berrien counties. 32. *C. platyphylla*
59. Leaves more than 20 mm wide, or less than 9 mm wide and over 15 cm long; inner band red-dotted or not; angles of culm narrowly winged or not.
60. Culms more than 2.5 mm wide at 5 cm from base; plants short-rhizomatous. 25. *C. lupulina*
60. Culms less than 2 mm wide at 5 cm from the base; plants caespitose.
61. Larger leaves over 17 mm wide; culm below inflorescence \pm 2 mm in diameter, very narrowly winged. 50. *C. albursina*
61. Larger leaves less than 15 mm wide; culm below inflorescence 1–1.5 mm in diameter, winged or not. [The next 3 species are closely related members of the *Laxiflorae* group and may not key out readily without fruit.]
62. Basal sheaths red-dotted. 51. *C. laxiculmis*
62. Basal sheaths not red-dotted.
63. Few dead basal leaves present, the basal sheaths and blades of previous year's growth decomposing rapidly and completely; free portion of ligule often not evident (*C. gracilescens* may occasionally key out here; it usually has an evident ligule). 52. *C. leptonervia*
63. Some dead leaves of previous year's growth usually present; free portion of ligule evident. 53. *C. laxiflora*
54. Leaf plicate ("V" shaped in cross section), not doubly folded, or doubly folded and the mid-lateral veins not distinct on basal half of leaf blade.
64. Inner band whitish and puckered below summit. 54. *C. sparganioides*
64. Inner band yellowish or not puckered below summit.
65. Larger leaves 5–7 mm wide; most frequent in the southern Lower Peninsula. 55. *C. cephaloidea*
65. Larger leaves 3.5–5 mm wide; throughout.
66. Spikelets interrupted, pedunculate.
67. Leaves \pm basal or with base of blades within 5 cm of base of plant; spikelets \pm ovoid. 41. *C. deweyana*
67. Leaves cauline, with base of blades mostly 5 cm or more above base of plant (excluding sheaths with shortened blades); spikelets obovoid or spherical.
68. Spikelets greenish-yellow to brownish; perigynia nerveless. 43. *C. aenea*
68. Spikelets silvery-green to pale brown; perigynia nerved on ventral face. 44. *C. argyrantha*
66. Spikelets not interrupted, sessile. 45. *C. cephalophora*

HABITATS AND GENERAL DISTRIBUTIONS

43. *C. aenea* Fern.—Dry, open ground or disturbed woods; Upper Peninsula and northern Lower Peninsula.
50. *C. albursina* Sheldon—Rich, moist beech-maple, mixed hardwood stands; throughout Lower Peninsula except for northeast quarter.
35. *C. amphibola* Steud.—Usually low woods; southern half of Lower Peninsula.
28. *C. arctata* Boott—Usually on moist ground in rich deciduous woods and wooded dunes; throughout.
44. *C. argyrantha* Tuckerman—Local in aspen woods, wooded dunes, and occasionally richer deciduous forests; scattered throughout.
20. *C. artitecta* Mack.—Woods and clearings, especially on sand dunes; most frequent in the southwest quarter of Lower Peninsula.
11. *C. backii* Boott—Local in open and second-growth woods; Upper Peninsula and northern Lower Peninsula.
37. *C. bromoides* Willd.—Low or upland woods; scattered throughout.
38. *C. brunnescens* (Pers.) Poir.—Very common and widespread in low woods, swamps, and bog borders, occasionally in upland woods; throughout.
2. *C. careyana* Dewey—Rich deciduous woods; southern half of Lower Peninsula.
55. *C. cephaloidea* (Dewey) Dewey—Rich deciduous woods; mainly scattered in southern half of Lower Peninsula.
45. *C. cephalophora* Willd.—Deciduous woods and thickets; common in southern half of Lower Peninsula.
22. *C. communis* Bailey—Deciduous woods, especially on sandy soil; throughout.
40. *C. convoluta* Mack.—Rich, upland beech-maple or oak woods; scattered throughout.
27. *C. crinita* Lam.—Swamp forests and other low deciduous forests; throughout.
7. *C. davisii* Schw. & Torrey—Floodplain forests and stream banks; widely scattered in southern Lower Peninsula.
21. *C. debilis* Michx.—Moist areas of all types, often in open hardwoods; scattered throughout.
41. *C. deweyana* Schw.—Forests of all kinds, particularly beech-maple; throughout.
49. *C. digitalis* Willd.—Rich, moist deciduous woods, occasionally drier oak woods; southern half of Lower Peninsula.
18. *C. emmonsii* Dewey—Sandy, open ground and wooded dunes; mainly in southern half of Lower Peninsula.
6. *C. formosa* Dewey—Rich beech-maple woods, wooded ravines, and occasionally open meadows; most frequent in the southeast quarter of Lower Peninsula.
14. *C. gracilescens* Steud.—Rich beech-maple, low oak-hickory, or other moist woods; southern half of Lower Peninsula.
15. *C. gracillima* Schw.—Beech-maple, oak-hickory, and coniferous woods; common throughout.
26. *C. grayi* Carey—Rich deciduous woods and wooded floodplains; most frequent in southern half of Lower Peninsula.
3. *C. gynandra* Schw.—Openings in low woods, thickets; Upper Peninsula and northern Lower Peninsula.
4. *C. hirsutella* Mack.—Upland oak woods, low open areas; southern half of Lower Peninsula.
5. *C. hirtifolia* Mack.—Rich deciduous woods; scattered throughout but most frequent in southern half of Lower Peninsula.
34. *C. hitchcockiana* Dewey—Rich beech-maple and alluvial woods; mainly scattered throughout Lower Peninsula.
24. *C. intumescens* Rudge—Low, wet woods and thickets; throughout.
10. *C. jamesii* Schw.—Rich deciduous woods, frequently beech-maple woods; southern half of the Lower Peninsula.
51. *C. laxiculmis* Schw.—Rich deciduous woods; southern half of Lower Peninsula.
53. *C. laxiflora* Lam.—Rich deciduous woods, occasionally open woodlands; mainly scattered throughout Lower Peninsula. Includes *C. blanda* Dewey.

52. *C. leptoneuria* Fern.—Rich deciduous or mixed woods; throughout, common northward.
25. *C. lupulina* Willd.—Swamp forests and depressions in woods; throughout.
46. *C. muhlenbergii* Willd.—Sandy fields, woods, and borders of woods; throughout Lower Peninsula, uncommon in the Upper Peninsula and northern third of Lower Peninsula.
31. *C. muskingumensis* Schw.—Deciduous swamps and floodplain forests; southern Lower Peninsula.
16. *C. oligocarpa* Willd.—Rich deciduous woods; rare, restricted to southernmost counties.
13. *C. ormostachya* Wieg.—Beech-maple, hemlock-hardwood, and sandy aspen-red pine woodlands; Upper Peninsula and northern half of Lower Peninsula.
17. *C. peckii* Howe—Beech-maple-hemlock woods, occasionally open woods; Upper Peninsula and northern half of Lower Peninsula.
23. *C. pedunculata* Willd.—Beech-maple woods; common throughout; fruiting in May.
19. *C. pensylvanica* Lam.—Dry deciduous woods and dry, sandy, open ground; common throughout.
1. *C. plantaginea* Lam.—Usually in rich deciduous woods, especially beech-maple forests; throughout.
32. *C. platyphylla* Carey—Beech-maple woods; very rare, only known from St. Clair and Berrien counties in Michigan.
30. *C. prasina* Wahl.—Rich deciduous, usually low, woods; mainly scattered in the southern half of Lower Peninsula.
36. *C. projecta* Mack.—Wet meadows and swamp forests; throughout.
12. *C. retrorsa* Schw.—Swamp forests and other low, shaded areas; throughout.
39. *C. rosea* Willd.—Rich, moist, woods; scattered throughout.
48. *C. scabrata* Schw.—Wet areas, especially those in rich deciduous woods; scattered throughout.
54. *C. sparganioides* Willd.—Rich beech-maple woods, occasionally oak-hickory or floodplain forests; throughout Lower Peninsula.
47. *C. sprengelii* Spreng.—Woods and thickets; widely scattered throughout.
33. *C. stipata* Willd.—Very common in moist, shaded areas; throughout.
8. *C. swanii* (Fern.) Mack.—Low, rich deciduous woods or occasionally dry oak woods; southern half of Lower Peninsula.
42. *C. tenera* Dewey—Various open or wooded habitats; throughout.
9. *C. virescens* Willd.—Usually in dry, sandy woods; uncommon, southern half of Lower Peninsula, especially along Lake Michigan shore.
29. *C. woodii* Dewey—Beech-maple or low deciduous woods; throughout, common in southern Lower Peninsula; fruiting in May.

The construction of this key was based largely on the well-curated collections of Carices in the University of Michigan Herbarium (MICH). For information on habitats and distributions I relied heavily on Voss (1972), as well as the knowledge of Drs. Edward G. Voss and Anton A. Reznicek. I would like to thank Janice G. Lacy for the illustration and Drs. Voss and Reznicek, who criticized the manuscript and offered many useful suggestions.

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REVIEW

THE BOREAL ECOSYSTEM. By James A. Larsen. Academic Press, New York, 1980. 500 pp. \$45.00.

Larsen presents a comprehensive overview of the boreal forest in North America, with much data from his own community analyses "in central Canada," i.e. Manitoba and Ontario but with additional study sites in Keewatin, Saskatchewan, Minnesota, and Wisconsin—though not thus identified in fig. 22 (and cf. fig. 27). But very little explicit information is from as far south as Lake Superior (pp. 172–176 in a chapter giving a broad view of "Boreal Communities and Ecosystems" across the continent, and two paragraphs on p. 398 with a single reference on the plant-moose-wolf system on Isle Royale but nothing on moose and sodium either here or under nutrient cycling). The basic subjects of climate and soils are dealt with in chapters which, like others, have copious lists of references, especially journal articles, and are valuable compilations. For general student use, a very helpful chapter is "Boreal Communities and Ecosystems: Local Variation," which reviews topics like competition, succession, permafrost, and fire, and concludes with the sage observation: "At the present time, it can only be said that, given the state of development of our understanding of the boreal ecosystem, much remains to be learned at every level of boreal ecology."

The author is firmly in the Wisconsin "continuum" school concerning plant communities, although persistent use of an invented plural "continuuua" implies a lack of schooling—or of editing. A conscientious editor might also have helped to reduce an overly repetitive style, even in the same chapter. Why, for instance, should there be a long quotation from Carleton and Maycock on p. 322 and then, as if a new idea, repetition of the first paragraph in most of the same words on p. 334? Why are the same 20 species noted by Agassiz on the north shore of Lake Superior as well as in Europe listed on both p. 164 and pp. 174–175 (in both instances including *Loiseleuria procumbens*, which was surely a misidentification)? Appendix VI is a list of "Species in Boreal Forest Literature," in which (apart from too many spelling and punctuation errors) it is surprising to see such decidedly non-boreal-forest species as *Carex pensylvanica*, *C. woodii*, and *Lathyrus japonicus*. Two species of *Andromeda* are listed here, although in the text only once did I find *A. glaucophylla* mentioned; one must assume that whenever the author refers to *A. polifolia* as a species of the boreal forest he is making the taxonomic judgment (as a few people do) to lump *A. glaucophylla* with it!

"Fortunately," says the author, "except for a relatively few forest pests, most insects occur in comparatively small numbers"—and the rest of the section on "Role of Insects" is clearly addressed to the problem of pests with not even a nod toward the notion that some insects may be beneficial or that problems confronted by pollinators may affect flora and vegetation. Except for a mere passing reference under the nitrogen cycle (p. 361), there is nowhere a discussion of mycorrhizae; although a number of pages are devoted to lichens, fungi are apparently considered relatively unimportant. Another incredible illustration of an unconscious attitude that tree life stops at ground level is the assertion that after fire "even if the tree is killed, new sprouts arise abundantly from the roots of the dead tree." Now, either the tree is dead, or the roots have life and sprout. Or does the author really think that roots are not part of the tree?

In referring—as most palynologists do—to "climatic deterioration" and "worsening climatic conditions," the author takes a homocentric or "taxo-centric" point of view I deplore. What is "worsening" for man or beech may be ameliorating for spruce or fir! Why must our own biases as to what a "good" climate is affect descriptions of postglacial vegetation?

Altogether, this is a well illustrated and extensively documented work, concentrating on forests of northern Canada but useful to all who have an interest in how the great "north woods" functions.

—E. G. Voss

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A NEW GREEN ALGA, *COELASTRUM COSTATUM*
VAR. *SCHMIDLEI*, AND A REVIEW OF
COSTATE *COELASTRUM* SPECIES

Mason G. Fenwick

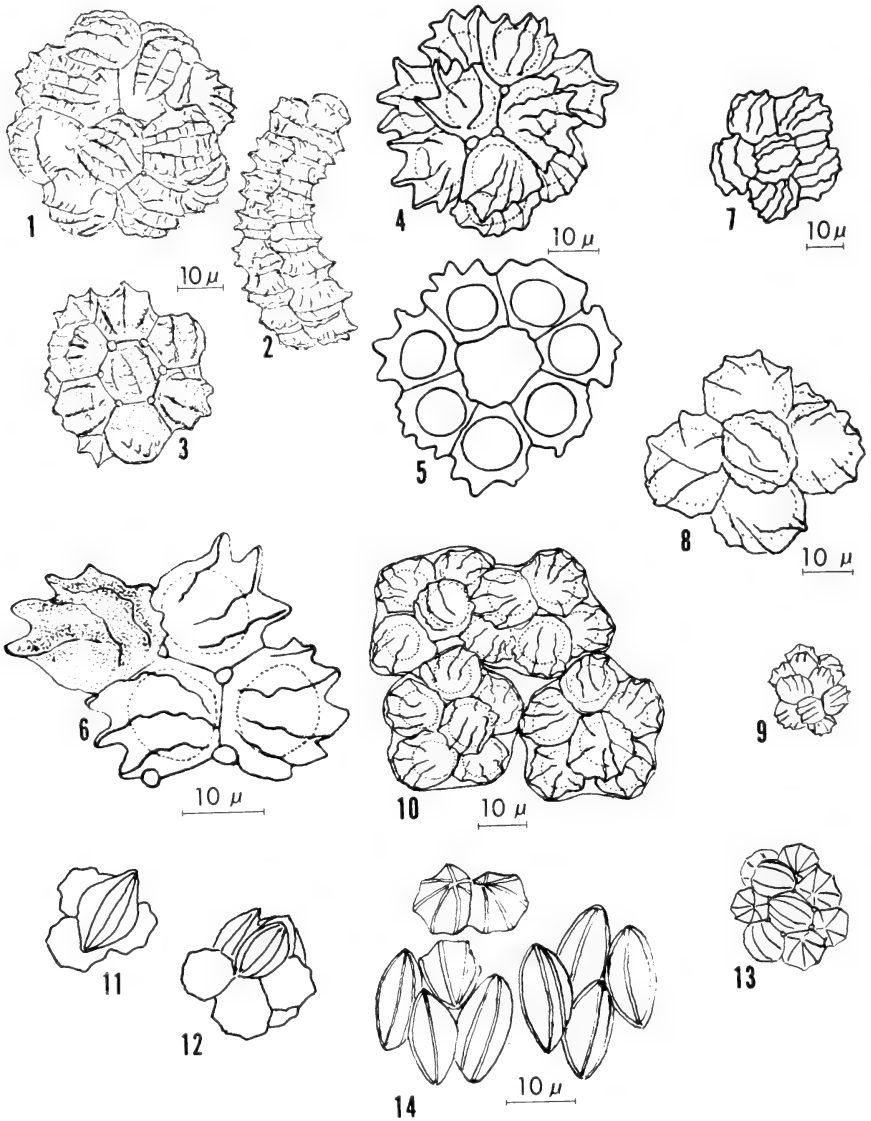
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Coelastrum costatum var. *schmidlei* var. nov. Cellulae costatae et ferrugineae ut in typo, sed non striatae inter costas.—Cells costate and orange-brown as in the typical variety but lacking striae between costas.—Type, Figs. 4, 5, 7, Port Radium, Great Bear Lake, Northwest Territories, Canada.

The description of *Coelastrum costatum* (Schmidle) Korsch. (Figs. 1-3, from Korschikov, 1953) is translated from Ukrainian, as follows: The plants have spherical cells, with tightly adjoining, very thick surface membranes with 2-6 bulges looking like parallel ribs jagged at the edges: between them are smaller transverse ribs. Each cell is connected to 4 or 6 adjacent cells by thick but very short lateral extensions. Intercellular spaces are very small and hardly noticeable; the cells contain much oil of reddish color. Coenobia are spherical, usually composed of 8 or 16 cells. Species grown in the laboratory, in addition to other deviations, form 2-rowed *Scenedesmus*-shaped coenoba [reproduced here as fig. 2]. Cell diameters 10-15 μ m. Coenobia up to 45 μ m in diameter. The species was found in northern European USSR in *Sphagnum* bogs with filamentous algae and mosses.

The species proper has not been reported from the Americas, but the var. *schmidlei* was present in algal samples collected at Port Radium, near Great Bear Lake, by W. C. Steere et al., 1945, under a grant from the Office of Naval Research to the University of Michigan (Fenwick, 1966), in pools in association with *Utricularia*. During summers of 1955 and 1956, I found the same variety (figs. 6, 8, 10) in abundance in the northern part of the Lower Peninsula of Michigan, at the University of Michigan Biological Station, first in intestinal tracts of tadpoles and subsequently in a sedge-beach pool on the north shore of Douglas Lake at Sedge Point, where the tadpoles had been collected.

Schmidle (1898, p. 9, pl. 1, fig. 1) illustrated a plant (reproduced here as fig. 9) from Sweden, in Pite-Lappmark, "hoch alpen gefunden," and designated it as *Scenedesmus coelastroides* (Bohlin) Schmidle. He considered it, with some uncertainty, the same as Bohlin's *S. costatus* var. *coelastroides* 1893 (reproduced here as figs. 11, 12, redrawn from Chodat 1902, fig. 142). Schmidle said, "Die Stellung dieser Art ist nicht sicher; ich habe im Material vollig ausgebildete hohle *Coelastrum* Kugeln bei dieser Algen gesehen; die Zellen waren dabei durch 5-6 kurzen Seitarme wie bei *C. pulchrum* mit einander verbunden. Daneben sah ich freilich auch solide Kugeln." The variety described here (figs. 4-6, 8, 10) resembles Schmidle's illustration (see fig. 9). Schmidle did not show striae or



Figs. 1-3. *Coelastrum costatum* Korsch., redrawn from Korschikov's original illustrations (1953). 4, 5, 7. *Coelastrum costatum* var. *schmidlei*, type, Port Radium, Northwest Territories, Canada. 6, 8, 10. *Coelastrum costatum* var. *schmidlei* from Sedge Point, Douglas Lake, Mich. 9. *Scenedesmus coelastroides* (Bohlin) Schmidle, redrawn from the original illustration (Bohlin, 1898). 11-12. *Scenedesmus costatus* var. *coelastroides* Bohlin, as reproduced by Chodat (1902). *Coelastrum tallonii* Bourelly & Manguin, drawing received from Bourelly. 14. *Ennalax alpina* Pascher, redrawn from the original.

ribs between the costae, nor did he show costae converging to a point, as illustrated in Bohlin's *Scenedesmus costatus* var. *coelastroides* (see Figs. 11, 12). Smith (1916) stated that the above algae are not *Scenedesmus* but *Coelastrum* and considered them identical (even though the illustrations show that they are not alike). Rayss (1915) said that *Coelastrum bohlinii* Schmidle & Senn (in litt.), "n'est autre chose que *Scenedesmus costatus* var. *coelastroides* = *Scenedesmus coelastroides* (Bohlin) Schmidle, à coenobe globuleux." Korschikov (1953) illustrated *Coelastrum bohlinii*. (The figures given here as 11 and 12 are redrawn from Chodat's reproduction of Bohlin's original illustrations of the var. *coelastroides*.) Korschikov (1953) considered *S. costatus* var. *coelastroides* Bohlin and *S. coelastroides* (Bohlin) Schmidle as synonyms of *C. bohlinii* Schmidle & Senn.

Bourelly & Manguin (1950) described *Coelastrum tallonii*. Figure 13, provided by personal communication from Bourelly, shows that species to have a coenobium with fusiform cells with converging costae as in Bohlin's *S. costatus* var. *coelastroides* (fig. 12). Pascher's (1943) *Ennalax alpina* (reproduced as fig. 14) also resembles Bohlin's taxon (fig. 11). It thus appears from the iconography that *Ennalax alpina* Pascher (1943), *Scenedesmus costatus* var. *coelastroides* Bohlin (1893), and *Coelastrum tallonii* Bourelly & Manguin (1950) represent the same taxon. Schmidle's (1898) illustration of material which he referred, with uncertainty, to *Scenedesmus coelastroides* (Bohlin) Schmidle suggests that his plant belongs instead to *Coelastrum costatum* var. *schmidlei*.

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On the cover: *Livingston Bog*,
Cheboygan County, Michigan;
photo by Jeffrey Holcombe

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THE

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HOW ABOUT A WILD MEAL?

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✓ (1)

Gathering, preparing, and eating wild plants can be an exciting adventure and, in extreme situations, a means of survival. Our ultra-modern, technically-supported, stainless-steel world often makes us wonder if we have in us any of the pioneer spirit that sustained our adventuresome forebears. So we escape to the "great outdoors," away from superhighways, electric lights, and air conditioning. Our hurried and harried business world and production lines drive us to mountain retreats, serene forests, prairies, and seashores for a bit of fishing or bird and game hunting. As an alternative to these potentially destructive activities, hiking or back-packing into the wilderness has special appeal. All these activities may be combined with the delights of tastily prepared wild plants, and, should misfortune occur, a knowledge of edible wild plants could very well be life-saving.

Even a home-prepared meal may take on special zest if, instead of frozen peas, a dish of roadside greens is substituted. In fact, it was a recent experience of mine to be served an entire meal of wild foods in a setting of white linen, candlelight, and stereophonic music. The food was superb and led to the liveliest conversation imaginable. The evening will not soon be forgotten.

Shopping for Wild Plants

Wild plants for eating are more readily available than one might assume, and the best places are frequently close by. Roadsides, vacant fields and city lots, stream banks, marshy areas, fence rows, and some of the less dense wood lots are among the choice areas. Thick coniferous forests, mountainsides, and tropical isles yield fewer good edible specimens.

Learning to identify the edible plants in a tangle of growing vegetation can be a challenge, but with practice they can become as familiar and as readily identified as the kinds of produce displayed at the grocery store. Before preparing any wild food it is wise to heed Euell Gibbons' advice, "Never use any wild plant or creature for food until you have identified it and know it to be edible." Try learning one plant at a time and learn it well. You will have a reasonable menu in a surprisingly short time.

Wild plants, of course, never occur in the abundance of plants in cultivation. Plants are a renewable resource if we take only what we need and leave enough for the plants to propagate themselves again. We also have an obligation to familiarize ourselves with plants protected by state laws. They must not be used, and we must be careful not to harm them when removing other plants close by.



Wild food enthusiasts are familiar with the books and articles by the late Euell Gibbons shown here with his wife, Freda, who was his companion during many years of foraging in wilderness areas across the country. The photograph was given the author by Mrs. Gibbons.

Nature has been very generous in producing tasty plants. Most plants can be eaten without harm even though they may not be exactly palatable. There are, however, a few precautions in gathering wild foods. First, be sure you have permission to collect before trespassing on private property. Next, observe the area from which you are gathering. Polluted waters in streams and marshy areas can contaminate plants growing there. Such plants must never be eaten raw. Some plants, normally edible, become dangerous if sprayed with pesticides or if fertilizer residues are adhering to them. Be careful therefore when gathering at roadsides or in areas adjacent to private property that may have been chemically treated in any way. Finally, be aware that plants can be safe or dangerous to humans, and in fact *individuals may differ in their reactions*. Occasionally one person will suffer from eating a plant not normally regarded as upsetting or poisonous to other adults. Allergies caused by wind-blown pollen or spores and dermatitis caused by direct or indirect contact can cause considerable temporary misery.

Culinary Safety

Usually large amounts of most poisonous plants must be consumed before they become life threatening. This does not mean, however, that they will not cause a great deal of gastric discomfort even though not fatal. A few good rules to avoid poisoning while gathering or eating wild plants are:

1. Eat only the plants you know are edible.
2. Do not rely on pets, birds, or wild animals to indicate safe plants.
3. Do not use parts of unknown plants as skewers, roasting sticks, toothpicks, straws, or for "nibbling." A whole troop of Boy Scouts became very ill when they used the hollow stems of poison hemlock for milk straws.
4. Learn to recognize frequently encountered dangerous plants such as poison ivy, Death Angel mushrooms, and poisonous nightshades and hemlocks.
5. Be aware that children are more susceptible to toxic substances than adults and may be affected by smaller quantities.

With these precautions in mind we can select the plants most pleasing to us for foods.

Culinary Instructions

A number of good cookbooks are available for specific recipes, but a few generalizations for preparing wild plants may be made. Wild plants should always be thoroughly washed and damaged parts removed. Be prepared to spend more time cooking wild plants than you would garden varieties. Many wild plants retain the tough veins, intense flavors, or inedible juices that have been bred out of their cultivated relatives; eliminating these features often requires extra steps in cooking.

Edible wild plants have their own distinctive flavors, so that when a recipe says to cook a plant like asparagus or like spinach it means only that the method of preparation is the same; the flavor will be quite different and probably more intense.

You can freeze many of the plants for future use or preserve them by a pioneer method of dehydration. Mash or press leaves, stems, or roots into flat cakes and allow them to dry in a warm, dry, shaded spot. The dried cakes will store well without refrigeration.

Annuals may be pulled up entirely, but do not needlessly disturb the roots of perennials and leave enough leaves and stems to allow them to recover. In all cases, take only what you will use and only as much as the plant population can tolerate without threatening its re-establishment.

Wild Food Plants

Wild plants can be served in a number of ways just as domesticated plants can. Some of the leafy ones make excellent salad greens or can be cooked, spinach-like, as potherbs. Because of strong flavors, latex-like juices, or glandular bristles, leaves and stems sometimes need to be treated to several changes of boiling water before they are edible.

Pollen and tiny seeds can be added as supplements or extenders to wheat flour or for the interesting flavors and textures they impart. Whole roots of some plants can be ground as a flour substitute. Roots may also be used as boiled vegetables similar to potatoes and carrots or ground and boiled as coffee substitutes. Other beverages may be made from flowers, fruits, and bark yielding lemonade-like flavors.

French fried or batter-dipped flowers, buds, leaves, roots and pods usually suit the fussiest appetites. And who can resist such delicacies as fresh wild strawberries or blueberries or their jellies and jams?

Shopping for a Wild Meal—The Supermarket Plants

It is nearly impossible to catalogue all the edible wild plants, but some of them stand out because of their abundance, wide ranges, length of season, or exceptional palatability. One such plant is the cattail (*Typha latifolia*) designated by Euell Gibbons, the late wild-food advocate, as the “supermarket of the swamp” because of its many edible parts and year-around availability. Early in the spring when new shoots are a foot or so high you can start enjoying the first of the foods of the cattail. Grasp the shoot at the base and give a quick pull, and the shoot will break off. If peeled down to the succulent core, it can be eaten as a fresh crunchy vegetable or cooked until tender and served with butter. These young shoots will continue to be available well into the summer in marshy areas where large populations of cattails thrive.

The tiny monoecious flowers of the cattail are arranged around a hotdog-sized columnar core, with the staminate flowers (which produce pollen) forming a distinct region of the spike above the pistillate portion (which produces seeds). The immature flower spikes can be picked and removed from their sheaths and then boiled as a vegetable that is as good as or (some say) better than corn-on-the-cob. Somewhat later in the season, pollen will begin to drift from the spikes as the flowers mature. Abundant quantities of pollen can be collected by shaking the spikes into a plastic bag. When equal amounts of pollen and wheat flour are combined in recipes, beautifully yellow and tasty pancakes, biscuits, or bread can be made. Unfortunately pollen tends to mold when stored, so collect only as much as you can use at one time or freeze the excess for future use.

The cattail rootstock can be used at any time of year. The core can be dried and ground into a flour, and the new leading ends of the rootstock just below the ground surface can be peeled and eaten raw or cooked like potatoes. It is best to serve them in early spring or late fall when (it is said) frost makes them more tender. The junctions of rootstock and young leaf shoots are especially good and can be used in a number of tasty dishes. And if that isn't enough, cattail down can fill the softest pillow or make a pain-relieving compress for a burn. The cattail is truly versatile.

A word of caution, though, if you look for young cattail shoots in early spring. Don't confuse them with *Iris versicolor*, which often grows along with cattails. A bit of the *Iris* rootstock has a pretty good cathartic effect.

Several other plants may be considered “supermarket plants.” The common milkweed (*Asclepias syriaca*), the escaped daylily (*Hemerocallis fulva*), and the ubiquitous dandelion (*Taraxacum officinale*) are three that qualify.

Milkweed is found abundantly in open fields. The name is derived from the bitter milky juice that the plant produces. This latex contains poisonous resins and glycosides that in quantity disrupt normal heart rhythm and other physiological functions, and so it is important to remove most of the juice in boiling water. Cold water solidifies the juice, so be sure to plunge the plants

directly into boiling water. Boil gently for a few minutes, drain, and add fresh boiling water twice. Boil in the last water as long as necessary to produce tenderness.

Young shoots early in the spring make a delicious asparagus-like dish. Later and through the growing season the young leaves, shoots, and flower buds may be served as buttered vegetables. The clusters of buds mimic broccoli. Young green seed pods picked before silk forms on the seeds can be served as a boiled vegetable or dipped in egg and bread crumbs after boiling and lightly browned in oil.

Apparently the milky juice loses some of its tartness and toxicity if it is drained out of broken leaf veins and allowed to dry. The Indians found the rubbery residue a fairly good chewing gum, but it is pretty poor fare by present day standards.

The open flowers, so attractive to bees, can produce a sweet syrup. Simply boil six cups of flowers in one cup of water until thickened, then strain, discard the flowers, and use the syrup like honey.

The daylily, which long ago escaped cultivation to become a common roadside weed, is edible from root to shoot. The fleshy, peanut-sized tubers can be scrubbed, peeled, and eaten raw as delicious salad fare or cooked and served buttered or in a cream sauce. Well-established plants, either in the wild or in the garden, are not harmed by removing some of the tubers and will promptly grow new ones.

The tender inside stalk of the leafy shoots that first appear in the spring can be cut up for salads or boiled as a green vegetable. It is the flowers, though, that make the daylilies outstanding. They are commonly eaten in the Orient, and we can adopt some of their dishes for our tables. The unopened buds may be boiled and served like green beans. If you like batter-dipped fried foods, try these flowers either as buds or fully opened. A few flowers or buds added to soup will thicken it and add a delightful flavor. Individual daylily flowers are open only for a day, but even the wilted ones can be used in soups and stews to impart a slightly different flavor. The buds and flowers may be easily dried and stored for winter use. And if you can't eat all the flowers you pick, you can always make an attractive table centerpiece of the showy orange blossoms.

But, **a word of caution:** Dr. Florence Wagner of the University of Michigan and a group of workshop students had an unfortunate experience after a luncheon of wild foods in 1973. A bit of detective work narrowed the culprit down to sauteed daylily buds and/or tubers in a salad. All those who had eaten sizable amounts of daylilies suffered from nausea and diarrhea, one to the point of requiring hospitalization. Dr. Wagner has received reports of other sporadic cases of daylily poisoning, but until now no one has determined the toxic factor.

The *dent-de-lion* of the French is a well-known plant in this country just as in its native Europe, but Americans have been much more imaginative in devising recipes using the "lion-toothed" leaves, as well as roots and flowers. From April until fall the bright blossoms identify the plants along roadways, in fields, and on suburban lawns. "You cannot forget, if you would, those golden kisses all over the cheeks of the meadow, queerly called dandelions," so mused Henry Ward Beecher a century ago.

Who has not heard of salads, coffee, wine, and any number of nostrums produced from dandelions? Well, most of the claims you have heard for the dandelion are true! Even the name *Taraxacum officinale*, derived from Greek and Latin, alludes to its medicinal properties as a remedy for a wide range of "disorders."*

Nutritionally it's supposed to be especially good for you. How good? Here is how favorably it compares with several other foods known for their nutritional value:

100 g edible portion	Calories	Protein	Calcium	Phosphorus	Iron	Potassium	Vitamins	
							A (Intern. units)	C
Raw dandelions	45	2.7 g	187 mg	66 mg	3.1 mg	397 mg	14,000	35
Raw spinach	19	2.2	58	46	2.6	795	4,300	30
Sunflower seeds	560	24.0	120	837	7.1	920	50	0
Raw watercress	79	1.4	4	65	6.0	500	0	1
Raw mushrooms	28	2.7	6	116	.8	414	0	3

The leaves and flowers are most often used. Young leaves can be eaten raw in a salad or cooked in a number of tasty dishes. The flower heads can be sauteed, added to salads, or fermented to produce wine. They also make a delicious and beautiful yellow jelly. The roots, often used for their supposed medicinal properties, can be roasted and ground for coffee or boiled and sauteed as a vegetable, eaten sparingly because it is laxative. Avoid eating the older tough roots, the bitter aged leaves, and flower heads in transition to "Santa Clauses." The fuzzy-headed flower stalks belong in the domain of childhood amusements.

Salad Plants and Potherbs

In addition to the "supermarket" plants, there is a wide selection of others of more limited use, most of which are used for one or another especially fine attribute. The choices vary with geographic location and specific habitat. The plants may be considered useful as salad materials, potherbs, root vegetables, hot or cold beverages or wine, edible fruits, and special treats.

We'll take a brief look at some of the better choices. The accompanying chart is a compendium of information from a number of sources recommending these plants as wild foods.

*Our forebears decided that many of the medicinal properties of plants were revealed by the appearance of the plants. Known as the Doctrine of Signatures, the belief that a plant or plant part resembles the part of the human body or medical problem which it cures or alleviates probably dates back to prehistoric times. It is still accepted to some extent in many parts of the world. Thus the cloudy juice of the dandelion was associated with digestive or other internal problems and a poultice of *dent-de-lion* leaves was used to relieve a toothache. The liver-shaped leaves of *Hepatica* were used for liver ailments, but some other associations require more than a little imagination. Interestingly enough, some of these plants do affect the parts of the body they resemble, and treatments which worked were passed down from one generation to the next. Apparently no one bothered to remember those that were ineffective.

	Type of Dish													Parts Used								Habitat		Danger:
	soups, stews	root vegetable	breadstuffs	potherbs	salads	pickles, relishes	syrups, sugars	confections	beverages	fresh fruit	jelly, jam	chewing gum	roots	stems	leaves	buds	flowers	seeds	fruit	woods	fields, roadsides	marshes		
Arrowleaf (Sagittaria)		X								X			X		X				X	X		X		
Blueberry (Vaccinium)				X	X										X					X				
Bracken fern (Pteridium aquilinum)		X		X	X								X		X					X				
Burdock (Arctium minus, lappa)		X		X	X								X		X					X				
Cattail (Typha latifolia)		X		X	X	X			X				X		X					X				
Chickory (Cichorium intybus)			X	X	X				X				X		X									
Clover (Trifolium)				X	X				X				X		X									
Dandelion (Taraxacum officinale)		X		X	X				X				X		X					X				
Daylily (Hemerocallis fulva)		X		X	X				X				X		X					X				
Elderberry (Sambucus canadensis)		X		X	X				X				X		X					X				
Ginger, wild (Asarum canadense)				X									X		X									
Jack-in-the-Pulpit (Arisema triphyllum)			X	X									X		X					X				
Lamb's quarters (Chenopodium album)			X	X									X		X					X				
Mayapple (Podophyllum peltatum)				X					X						X									
Milkweed (Asclepias syriaca)		X		X		X						X			X					X				
Nettle (Urtica dioica)															X									
Nightshade (Solanum dulcamara)											X		X		X									
Onion (Allium)		X			X								X		X					X				
Poke (Phytolacca americana)				X											X									
Purslane (Portulaca oleracea)				X	X										X									
Queen Anne's lace (Daucus carota)		X											X		X									
Raspberry (Rubus)																								
Salsify (Tragopogon)		X		X								X	X		X									
Sassafras (Sassafras albidum)					X								X		X					X				
Spring Beauty (Claytonia virginica)		X			X				X				X		X					X				
Strawberry (Fragaria)																				X				
Sumac (Rhus typhina)																				X				
Watercress (Nasturtium officinale)		X		X	X										X					X				
Wintercress (Barbarea vulgaris)		X		X	X										X					X				

Among the plants suitable for salad greens are a number of species of the mustard family (*Cruciferae*). Winter cress or yellow rocket (*Barbarea vulgaris*) that brightens fallow fields with an icing of yellow in the spring can be picked in the winter from under the snow, when it is at its best. By the time the sun is approaching the spring equinox, the leaves will have developed a bitter taste.

A close relative is the aquatic watercress (*Nasturtium officinale*). Classically served at "ladies' teas" with cream cheese in nut-bread sandwiches, it tends to grow in slow-moving waters that may present an unexpected danger from pollution. Even commercially marketed watercress can be contaminated, and so you should soak the plants about 20 minutes in disinfecting water. You can use water-purification tablets, following directions on the package, or simply add a small spoonful of bleach to a sinkful of water. You may wish to follow this soaking with a rinse in salted water to kill tiny aquatic organisms clinging unnoticed to the leaves. In a final rinse in running water they will be washed away and you can enjoy your now safe-to-eat greens as salad fare or in delicious and beautifully colored soups.

Purslane (*Portulaca oleracea*) was a favorite wild food plant of the early colonists, but today it is usually looked upon with disdain as a spreading garden weed. Its young leafy stems make a tasty addition to a green salad. Related species growing along seashores often have a slightly salty taste. The older, large stems can be served as a cooked vegetable, added to soups, or even pickled, and the minute black seeds are often used as a flour extender or enhancer.

And what is a salad without a bit of onion (*Allium* spp.) in it? A wonderful selection of nearly 80 species grow wild in the United States, each with its own distinctive flavor. The wild onions, leeks, and garlics often grow abundantly in some places and can be eaten as salad or in any number of cooked dishes much like their domesticated relatives.

The family to which spinach, beets, and Swiss chard belong also contains one of the tastiest wild plants, the lamb's quarters (*Chenopodium album*). It frequently grows as a rank weed in waste places, but in its younger stages it is a good salad green or an incomparable potherb. The greens may also be gathered during the growing season and frozen, as you would spinach, for a mid-winter treat. Later you can gather the seeds and, after grinding them, add them to flour for some tasty biscuits.

In spite of deceptive appearances, poke (*Phytolacca americana*), bracken fern (*Pteridium aquilinum*), and stinging nettle (*Urtica dioica*) are also excellent potherbs. In fact, Euell Gibbons wrote that poke is the best-known and most widely-used wild vegetable in America, a claim that would be difficult to disprove. It is even available as a canned vegetable in some southern states. It must be reasonably popular since recipes for it are often found in wild-plant cookbooks. However, *only the young spring sprouts may be eaten*. The mature plant with its spectacular 6-foot magenta stems and deep-purple berries produces a strong emetic effect if any part of the plant is eaten, the roots and seeds being especially poisonous. If you gather seeds or handle the mature plants for any reason it is advisable to wear gloves because the plant juices contain substances that can be absorbed through the skin, especially in cuts and abrasions, and cause serious blood disorders. These are often difficult to diagnose because they mimic other medical problems.

Stinging nettle and bracken fern should also be used just as they emerge from the soil. Brackens, like all ferns, produce a fiddlehead or crosier that unrolls as the frond (leaf) develops. It is covered with a brownish fuzz that can be removed by pulling the fiddlehead through a closed hand. It is not likely that the coarse mature fronds would ever tempt anyone to nibble, but resist any such urges since at this stage they contain poisons that have been fatal to grazing horses and cattle. In fact, wild food enthusiasts are likely to substitute ostrich ferns (*Pteretis pensylvanica*) for bracken ferns these days since the ostrich fern croziers do not seem to contain any potentially toxic or harmful substances.

The hypodermic-like hairs on the stinging nettle make gloves necessary for picking, but the tender young shoots can be cooked as a delicious vitamin-rich potherb. A couple of changes of cooking water will completely remove the dermatitis-causing component in the hairs. Try the leaves with a dollop of sour cream sprinkled with chives.

Edible Roots

Roots are often available throughout the year which is usually not true of above-ground parts. The wild carrot or Queen Anne's Lace is the same species as the domesticated carrot. The carrots of our gardens are varieties of *Daucus carota* selected for size, color, and flavor. If they escape cultivation, they often give rise to new plants that revert to the native form in which the root is pale yellow, thin, and rather tough, but still edible. Added to soups or served with lots of butter and seasonings, they become reasonably palatable.

An occasionally encountered plant similar in appearance to the carrot is its deadly relative *Conium maculatum*, the poison hemlock. It too has a sturdy taproot but must *not* be eaten because of its poisonous juices. (Further discussion on the dangerous members of this family is in a following section.)

Perfectly safe are the first-year roots of burdock (*Arctium minus* or *A. lappa*). They have a distinct potato-like quality and may be used as substitutes in potato recipes. The Japanese have long favored this root, which they call gobo, and use it in sukiyaki and other dishes. American pioneers thought the roots had medicinal effects and used them for everything from skin irritations to pleurisy or even as an aphrodisiac. When digging the roots don't discard the youngest, tender leaf bases. These petioles look like rhubarb but are green; they are usually boiled and served as a vegetable in a number of excellent recipes.

A dozen species of the aquatic *Sagittaria* share the common names of arrowhead, wapato, or duck potato. *Sagittaria* plants are so often mentioned in connection with the travels of Lewis and Clark and other explorers that one wonders if the expeditions would have survived at all without the nourishing wapato. Reportedly Indians accompanying an expedition waded in the water and dug out the tubers with their toes. The tubers would float to the surface and be gathered in following canoes. Having tried tuber digging, I am impressed with the strength those Indians must have had in their feet. The tubers resemble potatoes in taste and texture and can be used in similar ways.

If your palate craves a bit of seafood, try the root of *Tragopogon* spp. This large relative of the dandelion is known as goatsbeard, salsify, and vegetable oyster, the last because its taste is almost identical to that of cooked oysters. It

is frequently cultivated and harvested in the fall. The milky juice in the stems can be coagulated into a passable chewing gum.

The tiny tubers of spring beauty (*Claytonia virginica*), often called fairy potatoes, are a real taste-treat. However, since it takes so many of them to produce a meal-sized portion, one should either have a very large supply of them or be near starvation before digging meal-sized quantities of them.

The wild ginger (*Asarum canadense*), common on the floor of a deciduous forest, has a pungent, aromatic creeping rootstock that has long been in use in medicinal preparations for a wide range of ailments. If you have overindulged in your meal of wild foods, you'll find that candied ginger is an anti-flatulatory so you can satisfy a sweet tooth and ease the discomfort of overeating at the same time.

In some parts of the country, narcissus, daffodils, and hyacinths have escaped their garden habitats and naturalized themselves in meadows and near streams and woodlots in company with smaller native American bulbous plants. The bulbs look so much like onions that it is hard to believe that they are not as edible. However, they may be extremely dangerous, causing nausea, vomiting, diarrhea, trembling, convulsions, and sometimes death. A good rule-of-thumb for selecting edible bulbs is to choose only those with the characteristic strong onion or garlic scent. Any other bulb must not be eaten until it is accurately identified and its safety assured.

Beverages and Fruits

Quite a few plants produce clear, tasty beverages. The best however are dried clover flowers (*Trifolium* spp.) and sassafras roots (*Sassafras albidum*) for tea-like drinks; dried and ground roots of chicory (*Cichorium intybus*) and dandelion (*Taraxacum officinale*) for coffee substitutes; steeped sumac fruits (*Rhus typhina*) for a pink lemonade; and elderberry fruits (*Sambucus canadensis*) or dandelion flowers for wine.

Elderberry flowers and fruits can be used for so many tasty dishes that a word of caution is in order. Although the flowers and ripe fruits of the elderberry are perfectly safe to eat the unripe berries and the vegetative parts of the shrub contain alkaloids that can cause nausea and vomiting and therefore should not be used or you may be accused of having "Arsenic and Old Lace" proclivities. A favorite and safe confection is fritters of batter-dipped elderflowers browned lightly in oil and served sprinkled with powdered sugar and orange juice. Elderberries are usually so sweet that when used in pies a bit of vinegar is often added to reduce the sweetness; they may be combined with the juice of sumac fruits to make a just-right tasting jelly.

The sassafras tree was one of the first native plants to be recognized by early settlers for its unique spicy flavor and supposed medicinal properties. It has been widely used over the years, but recent reports of a carcinogenic agent in sassafras have resulted in removing the commercially sold packages of roots from many markets. Sassafras oil contains safrole, which is also found in the oils of anise, camphor, mace, and ginger. In laboratory tests, when safrole oils were added to the diets of rats in concentrations of 0.5-1.0% of their daily food

allotment the rats developed non-cancerous liver tumors. Authorities agree that humans would have to eat large quantities of sassafras before possibly dangerous levels would be reached.

Berry picking and eating is a favorite pastime. Any of the raspberry-like fruits (*Rubus* spp.), blueberries and huckleberries (*Vaccinium* spp.), strawberries (*Fragaria* spp.), and the serviceberry (*Amelanchier canadensis*) make wonderful nibbling as one walks in dry fields or open woodlands, and they are equally good in pies, jams, jellies, or fruit compotes.

The round, yellow fruits of the mayapple (*Podophyllum peltatum*) may be eaten safely in small quantities but, if overindulged in or if not yet ripe, they will cause severe indigestion.

Gastric distress and poisoning may also result from eating unripe fruits of bittersweet nightshade (*Solanum dulcamara*) and its relative the ground cherry (*Physalis obscura*), although the ripe fruits are said to be edible. There may be individual sensitivity in this case. The unripe fruits of many other species of plants may be dangerous even though ripe fruits may be completely harmless. It is best to avoid those for which identification is not certain and eat only small amounts the first time you try those you think are safe.

Another family of plants that consists of both edible and dangerously poisonous members is the Umbelliferae or parsley family. Carrots, parsnips, celery, and the flavorful herbs parsley, anise, dill, and fennel produce the same umbrella-like head of flowers as do the deadly-poisonous water hemlock (*Cicuta maculata*) and poison hemlock (*Conium maculatum*). Poisonous alkaloids in the hemlocks cause severe gastrointestinal distress or death when fresh roots, stems, or leaves are eaten. The alkaloids are, however, destroyed by drying. The harmless sweet cicely (*Osmorhiza longistylis*) and cow parsnip (*Heracleum lanatum*) are remarkably similar to their poisonous relatives, and so if you are not positively sure of your identification, leave them all strictly alone. Remember, Socrates died from one of them.

Mushrooms—Edible and Poisonous

No discussion of edible wild plants would be complete without mentioning mushrooms, some of which are delectable foods and some digestively upsetting if not deadly poisonous.

The spongy morels (*Morchella esculenta*) of our spring woodlands, the shelf-like oyster mushrooms (*Pleurotus ostreatus*) on dead trees, the puffballs which range in size from ping-pong balls (*Lycoperdon pyriforme*) to pumpkins (*Calvatia gigantea*), and the shaggy mane (*Coprinus comatus*) and its relatives are commonly-eaten fungi, sometimes even sold in markets.

But beware! If gathering in the wild, be sure you can recognize the deadly angel of death (*Amanita verna*) and fly agaric (*Amanita muscaria*). All the amanitas have a ring (annulus) around the stem where the cap broke loose as it expanded, and a cup (volva) at the base. These are danger signs for these most deadly of mushrooms.

All mushrooms must be accurately identified to determine those which may be eaten safely. Some species may not be deadly but can cause severe

unpleasant symptoms. Since the toxic juices in mushrooms exude rather easily through the tender and easily bruised exteriors, mushrooms that are gathered should not be mixed together in a bag or basket since poisonous ones can contaminate non-poisonous ones even though separated from each other later.

Despite all the 'old wives' tests for distinguishing edible mushrooms from poisonous toadstools there are *no* reliable ones and we would be wise to heed these lines:

There are old mushroom hunters
And there are bold mushroom hunters
But there are no old, bold mushroom hunters.

We hope this article interests you in the art of choosing and preparing edible wild plants. This information, however, is brief and not intended to serve as anything more than a look at folklore (which is notoriously unreliable) and present practices and to encourage a more complete study of wild plants for edible and medicinal purposes. The author assumes no responsibility for the results of using any wild plants.

For more authoritative information on some of the plants discussed, consult the books listed below.

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245 THE BIOGEOCHEMISTRY OF BOG ECOSYSTEMS AND THE CHEMICAL ECOLOGY OF SPHAGNUM []

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This paper critically reviews selected aspects of the biogeochemistry of bogs and the chemical ecology of *Sphagnum*. The following factors play a role in the chemistry of bogs: cation-exchange by living *Sphagnum* and peat, the net biological uptake of ions by vegetation, the oxidation and reduction of sulfur compounds, the production of soluble organic acids by *Sphagnum* and peat, and the hydrologic regime. Contrary to most reports in the literature, it has recently been discovered that the dissociation of organic acids can significantly affect the acid-base chemistry of bog ecosystems.

For the past 20 years most investigators have argued that the chemical ecology of *Sphagnum* is controlled by hydrogen-ion production resulting from the cation-exchange process. In this paper it is suggested that the dissociation of polygalacturonic acid, not the production of hydrogen ions by cation-exchange, is actually the more important process in *Sphagnum* ecology. It is also argued that a full understanding of the chemical ecology of this moss will not be possible until detailed experiments on resource ecology (i.e., growth responses to light, nutrients, pH, etc.) have been performed to determine the actual mechanisms by which *Sphagnum* compete with one another and with other plants.

Sphagnum bogs are best known as remarkable floral habitats, but they are also biogeochemical systems of striking complexity. In this paper I will review both the major chemical processes that determine, in part, the acid-base balance of bogs and the chemical ecology of *Sphagnum*. The following factors all play a role in the acid-base chemistry of a bog ecosystem: cation-exchange by living *Sphagnum* and peat, the chemistry of atmospheric precipitation, the net biological uptake of ions by vegetation, the oxidation and reduction of sulfur compounds, the production of soluble organic acids by *Sphagnum* and other plants, and the hydrologic regime (see Fig. 1).

Cation-exchange.

For nearly 20 years cation-exchange by *Sphagnum* has been considered the predominant chemical process controlling bog chemistry. Up to 21.5% of the dry weight of *Sphagnum* is polygalacturonic acid (PGA), commonly known as unesterified pectin (Spearing, 1972). Cation-exchange occurs when the hydrogen ions of this organic acid are exchanged for other cations in the environment (Ca^{2+} , Mg^{2+} , K^+ , Na^+ , etc.). In other words, a solution containing Ca^{2+} and SO_4^{2-} before cation exchange would become a solution of H_2SO_4 after cation-exchange. The cation-exchange capacity of *Sphagnum* (milliequivalents of cation exchanged/gram dry weight of plant material) increases, with respect to the cation exchange, with increasing atomic number and valence (i.e., $\text{Na}^+ < \text{K}^+ < \text{Ca}^{2+} < \text{Mg}^{2+}$), however, the cation-exchange capacity of Na^+ is only ca. 20% less than that of Ca^{2+} (Belkevich & Christova, 1968). The cation-exchange

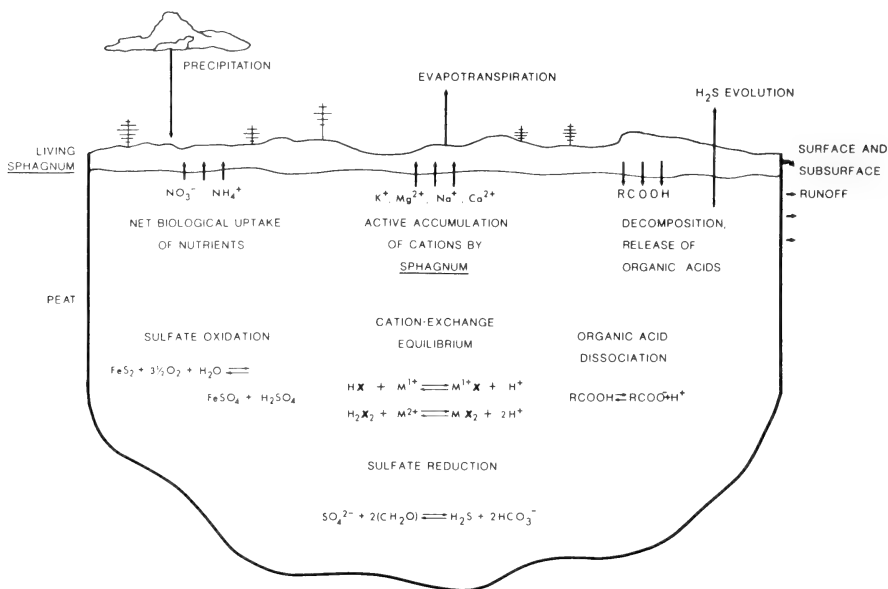


Fig. 1. Schematic representation of a bog ecosystem including chemical reactions occurring within the system that affect the acid-base balance. Major inputs and outputs to and from the bog ecosystem are also shown. Atmospheric precipitation contains SO_4^{2-} , H^+ , NO_3^- , NH_4^+ , Ca^{2+} , Na^+ , Cl^- , Mg^{2+} , K^+ (in rank order by equivalents for data collected at Pellston, Michigan). Surface and subsurface runoff from a bog has the same ions as atmospheric precipitation, but their rank order differs. Runoff also contains organic acids. This figure is modified from Hemond (1980).

capacity of living *Sphagnum* is ca. 1 meq/g dry wt. (Clymo, 1967). This value is similar to that of some clays (montmorillonite and vermiculite; Garrels & Christ, 1965, p. 271), but it is only one-tenth to one-third that of synthetic ion-exchange resins (Clymo, 1967). There is a strong correlation between the PGA content of particular species of *Sphagnum* and their cation-exchange capacity (Spearing, 1972).

Atmospheric precipitation.

Even though few data exist concerning the pH of atmospheric precipitation in North America prior to 1960, it is generally accepted that the hydrogen-ion content of precipitation falling on the eastern half of North America and northern Europe has increased markedly over the past 30 years (Likens et al., 1979). It is unlikely that atmospheric precipitation with a pH of 5.7 (the "natural" value of unpolluted precipitation; $[\text{H}^+] = 2 \mu\text{eq/liter}$) would have much effect on the chemistry of bogs. Acid precipitation ($\text{pH} \leq 5.7$; $[\text{H}^+] = 20 - 100 + \mu\text{eq/liter}$), on the other hand, plays a significant role in bog chemistry because atmospheric precipitation often becomes the major external source of both

nutrient and hydrogen ions to the bog ecosystem (Hemond, 1980). This has undoubtedly changed the acid-base chemistry of many bogs in that hydrogen-ion loading from the atmosphere now often predominates over internal sources of hydrogen-ion production (i.e., cation-exchange and the dissociation of organic acids).

The term "acid precipitation" is misleading because it overemphasizes the acidic nature of the substance. Precipitation of this sort also contains significant quantities of other cations and anions that are important in plant nutrition and energy transformation. Acid precipitation is a major source of nitrogen in regions where it occurs because ammonium and nitrate ions together make up ca. 25% of the total ionic content of this type of precipitation in terms of equivalents (based on National Atmospheric Deposition Program data for Pellston, Michigan, for July 1979 to September 1980). This value is similar to that for hydrogen ions. Sulfate ions are also abundant in acid precipitation (ca. 30%). Metal cations (Ca^{2+} , Mg^{2+} , Na^+ , K^+) are found in lower concentrations (ca. 15% altogether).

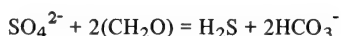
Net biological uptake of nutrient ions.

The net biological uptake of plant nutrients (Ca^{2+} , K^+ , NH_4^+ , NO_3^- , etc.) affects the acid-base balance of a bog ecosystem. Owing to the principle of electroneutrality, charge balance must be maintained between plants and their environment (Ruess, 1977). Therefore, when a plant takes up a positively charged ion (e.g., NH_4^+), a positively charged ion such as hydrogen (H^+) is released into the environment. Similarly, when a negatively charged ion is taken up by a plant a negatively charged ion such as hydroxide (OH^-) is produced. In a completely balanced ecosystem where nutrient uptake by plants equals nutrient regeneration through decomposition processes, the acid-base chemistry of the system is not affected by the differential uptake of anions and cations. However, few if any completely balanced ecosystems exist, and net biological uptake (NBU) of specific ions commonly occurs. NBU represents ionic and nonionic forms of a particular element stored or lost (via gaseous emissions) by the system. Net biological uptake equals the total biological uptake of a specific ion minus the quantity of that ion mineralized by decomposition and subsequently lost through output. NBU is a summary statistic that can be used to directly calculate net production of H^+ and OH^- resulting from nutrient uptake, because it is a measure of the change in chemical state that occurs within the system. Therefore, if the NBU for NO_3^- was one equivalent, one equivalent of OH^- was produced. Similarly, if the NBU for NH_4^+ was one equivalent, one equivalent of H^+ was produced.

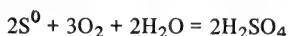
In practice net biological uptake of specific ions is calculated directly from the input-output budget for the bog ecosystem as a whole. If, for example, the sum of the NBU's for specific cations exceeds the sum of the NBU's for specific anions, the acidity of the system has increased because H^+ production has exceeded OH^- production. When OH^- production exceeds H^+ production, by the same mechanism, the system becomes more basic.

Oxidation and reduction of sulfur compounds.

Bogs are typically oxidizing environments near the surface, but they become reducing environments with depth. Under strongly anaerobic conditions sulfate reduction and pyrite (FeS_2) formation commonly occur. A generalized equation for sulfate reduction by bacteria is as follows (see Nriagu & Hem, 1978):



where SO_4^{2-} is balanced by metal cations or hydrogen ions and CH_2O represents organic matter. This reaction produces hydroxide ion which instantaneously combines with CO_2 to form H_2CO_3^- . The formation of pyrite and other reduced sulfur compounds proceeds rapidly if appropriate geochemical conditions prevail (Nriagu & Hem, 1978; Howarth & Teal, 1979). However, if the boundary between the oxidized and reduced zones in a bog were to shift (owing to changing hydrologic conditions?) such that pyrite and other reduced sulfur compounds were exposed to oxygen, bacterially mediated oxidation of these compounds would take place. Pyrite and elemental sulfur are oxidized according to the following generalized reactions (Wetzel, 1975):



Both these reactions produce sulfuric acid. In short, the acid-base balance of a bog ecosystem is strongly affected by biogeochemical transformations of sulfur compounds. Sulfate reduction under anaerobic conditions increases alkalinity by producing hydroxide ions, while pyrite oxidation under aerobic conditions increases acidity by producing hydrogen ions in the form of sulfuric acid.

Organic acids.

Bogs are often characterized by highly stained water rich in organic acids. These high molecular weight organic compounds of uncertain chemistry are collectively known as humic acids (see review in Wetzel, 1975). If the concentration of humic acids is sufficiently high, they become important in the acid-base balance of a bog. Dissociation of humic acids can be a major source of hydrogen ions.

Hydrologic regime.

The hydrologic regime determines within certain limits the concentration of ions and organic compounds dissolved in the water of a bog. Atmospheric precipitation and groundwater entering the bog ecosystem are concentrated by evaporation and evapotranspiration. The hydrologic balance of the system is also important because it, in part, determines the residence time of water (one

also needs to know the volume of water in the bog). Chemical concentrations change rapidly in bogs with short residence times and more slowly in bogs with longer residence times.

DISCUSSION

Most investigators consider only two of the six factors that can affect the acid-base balance of bogs to be important: cation-exchange and the oxidation of reduced sulfur compounds. Clymo (1963, 1964 & 1967) argues that cation-exchange by *Sphagnum* is by far the most important source of hydrogen ions for the bogs he studied. Before Clymo's papers were published, Gorham (1961) suggested that the acidity of a number of bogs in England could be explained by the oxidation of reduced sulfur compounds (both organic and inorganic). The investigations of Clymo and Gorham seemed appropriate at the time they were undertaken, but one cannot study the acid-base chemistry of a complex ecosystem by making a few field observations or performing a few isolated laboratory experiments. At the very minimum the study of the acid-base balance of a bog requires the construction of a moderately complete (electrically balanceable) input-output budget for mass and charge.

Perhaps not surprisingly, the results of the only complete biogeochemical mass balance study of a bog ecosystem currently available indicate that the acid-base balance of Thoreau's Bog in Massachusetts is primarily determined by the dissociation of organic acids (Hemond, 1980). Acid precipitation is the major source of hydrogen ions for Thoreau's Bog (ca. 10 times greater than cation-exchange), but hydrogen ions from this source are largely neutralized by hydroxide ions produced as a result of biologically-mediated sulfate reduction and net biological uptake of the nutrient component of acid precipitation. Cation-exchange was found to make only a modest contribution to the mineral acidity of the bog, and the oxidation of reduced sulfur compounds was not observed.

The chemical ecology of *Sphagnum*

The distribution of particular species of *Sphagnum* in bogs has been shown to be related to ambient pH and moisture. *Sphagnum* species growing highest above the water level of a bog (least moisture) have the highest PGA content (Spearing, 1972) and thus the greatest cation-exchange capacity. *Sphagnum* species growing highest in a bog also produce the lowest pH levels in their immediate environment. A gradient of increasing pH (decreasing H^+ concentration) is associated with various species from the top of hummocks down to the bottom of hollows or the water level of a bog. These relationships have been studied by Clymo (1963), Spearing (1972), Vitt et al. (1975), and Vitt & Slack (1975).

Even though cation-exchange is now widely accepted as the major chemical mechanism whereby species of *Sphagnum* control the pH of their immediate environment, I think there are compelling reasons to doubt that the cation-exchange mechanism could provide the degree of environmental control ascribed to it. Soon after the cation-exchange process was first studied in detail by

Anschütz & Gessner (1954), Ramaut (1955a, b) expressed doubts concerning the biological importance of the chemical process they had investigated. Ramaut argued that hydrogen-ion production is primarily under the physiological control of the plant. He demonstrated that living *Sphagna* can repeatedly decrease the pH of experimental solutions, while dead *Sphagna* can accomplish this feat but once. His experiments using live plants cannot be explained by the cation-exchange hypothesis because once base-saturation has occurred (i.e., all exchange sites are occupied by cations) no more hydrogen-ions could be produced, unless the cation-exchange sites were rechargeable. However, no mechanism is known for recharging the exchange-sites, and it is doubtful that sufficient new exchange sites could have been generated within the time interval Ramaut used in his experiments (24 hr.). Like Ramaut, I consider reduction of environmental pH by *Sphagna* to be an adaptive metabolic process similar to the homeostatic mechanisms that regulate the internal environment of organisms in general. I also believe it is unlikely that control over this adaptive function would be relinquished to a passive chemical process (cation-exchange) over which the moss has little control.

The cation-exchange process also depends on the availability of exchangeable cations, but in bogs cations come predominantly from atmospheric deposition. Given the vicissitudes of atmospheric deposition, one wonders if this really is a reliable source of cations. The water of the bog might provide a more reliable source of cations, but the species of *Sphagnum* with the greatest apparent requirement for exchangeable cations (producing the lowest pH levels) are located at the top of hummocks and farthest from the water. Even if we assume that sufficient cations are available to be exchanged for hydrogen ions, would the strong acids produced (H_2SO_4 , HCl) provide effective environmental control? This is not likely because strong acids are not chemical buffers and are readily soluble in water and thus probably quickly washed away from the plants that produce them, rendering them ineffective at regulating pH in the immediate environment. The cation-exchange hypothesis leads one to predict that a species of *Sphagnum* thriving at the top of hummocks and generating the lowest pH environments would have to contain considerably more Ca^{2+} and Mg^{2+} (in equivalents per million/unit dry weight) than species living at higher pH levels. But species living in both environments have essentially the same content of $\text{Ca}^{2+} + \text{Mg}^{2+}$. *Sphagnum fuscum*, a typical hummock species from a bog in Finland, had a $\text{Ca}^{2+} + \text{Mg}^{2+}$ content of 149 epm (equivalents per million)/unit dry wt. and *S. majus*, a species found in hollows, contained 151 epm/unit dry wt. (Aulio, 1980; see also Pakarinen, 1978). Aulio found some variation in the $\text{Ca}^{2+} + \text{Mg}^{2+}$ content among the 13 species investigated, but the observed variation was not habitat related. In other words, the most complete study of the mineral nutrient content of *Sphagnum* species undertaken to date provides no evidence that the cation-exchange process could account for the natural distribution of ions in *Sphagna*. However, Aulio's results might be explicable if a mechanism for re-charging cation-exchange sites were to be found.

Unlike the cation-exchange process, the direct production of PGA by plants may have many of the characteristics required to effect good environmental control. The production of this organic acid is completely under the

metabolic control of the plant. In *Sphagna* the carboxyl groups of the acid are exposed to the environment even though the acid itself remains associated with the plant (see Craigie & Maass, 1966). There is also a direct positive correlation between the PGA content of particular species of *Sphagnum* and ambient hydrogen-ion concentrations (Spearing, 1972), but this, of course, is also true for cation-exchange.

If we assume that cation-exchange is not the primary mechanism controlling environmental pH in *Sphagnum* species, then what is the ecological role of the cation-exchange process? In my opinion the relationship between PGA and exchangeable cations is somewhat analogous to the relationship between a chemical catalyst and a substance that poisons that catalyst. In other words, species of *Sphagnum* are able to control their environment despite rather than because of the cation-exchange process. Vitt et al. (1975) pointed out that the cation-exchange capacity of particular species of *Sphagnum* is a function of their PGA content and the degree of base saturation (i.e., the extent to which PGA has been "poisoned" by exchangeable cations). The "degree of base saturation" for particular species of *Sphagnum* is clearly an important parameter, but few data are available.

Another aspect of the relationship between PGA and the cation-exchange process that has received little attention is the buffer intensity of PGA associated with living *Sphagna*. If PGA is found to be a good buffer, a large quantity of strong acid would have to be produced as a result of cation-exchange in order to markedly change the ambient pH in the vicinity of a plant. In addition, if PGA is shown to be a good buffer it would provide strong support for the argument that the dissociation of PGA, not the cation-exchange process, is of primary importance in determining ambient pH.

In most organisms processes that potentially lower fitness, such as cation-exchange if it functions as suggested above, would be eliminated over evolutionary time. I think the cation-exchange process has survived because the advantages of controlling pH using PGA have outweighed the disadvantage of this organic acid's cation-exchange capacity. The major disadvantage is that exchangeable cations (bases) replace hydrogen ions on the exposed carboxyl groups of the moss, thereby reducing the effective concentration of carboxyl groups. This presumably makes it more difficult for the plants to control the pH of their immediate environment without diverting resources to the production of additional PGA.

Unfortunately, cation-exchange, PGA content, and mineral composition are the only chemical properties of *Sphagnum* that have received serious attention for more than 25 years. The acid-base chemistry of living *Sphagna* remains completely unknown and in need of attention. Even the effective dissociation constants for PGA associated with living mosses have not been determined. The only relevant data are those of Anschütz & Gessner (1954). Based on experiments using dried and powdered moss they reported that the organic compounds in the powder were undissociated (and thus of no ecological significance) at the pH of distilled water. Their work needs to be repeated using living moss as well. We must keep in mind that Hemond (1980) found that organic acids are primarily responsible for the pH of the bog he studied, despite the numerous

published speculations favoring strong acids produced as a consequence of the cation-exchange process.

The importance of resource competition and resource gradients
for the ecology of *Sphagnum*.

If *Sphagna* are similar ecologically to phytoplankton and higher plants (Tilman, 1982), it will eventually be shown that ambient hydrogen-ion concentrations (pH) play a secondary role in the moss ecology. Plants do not compete for pH any more than they compete for temperature, but these environmental variables can change growth kinetics with respect to a number of limiting resources. Thus the ability to control environmental pH may be tantamount to the ability to influence the results of competition for limiting resources.

It has been demonstrated theoretically and experimentally that at least two potentially limiting resources are involved when organisms compete along a resource gradient in space or time (Kilham & Tilman, 1979). Two potentially limiting resources are required because plant species segregate along a resource gradient owing to differences in their ability to utilize each resource and convert resources into growth (i.e., biomass, etc.). If only one resource were involved, the most efficient species would reduce the ambient resource level of the most limiting resource to an extremely low value. Thus, the most efficient species would outcompete other species along a resource gradient (i.e., species that grow better at higher resource levels).

In order to investigate resource competition among bog plants one would first have to identify which resources are potentially the most limiting. These might include light, water, potassium, phosphorus, nitrogen, etc. Once the primary limiting resources were identified, one could design a series of experiments to determine the kinetics of resource-limited growth for each species and each primary resource. In the case of *Sphagnum* species one would also need to determine the effect of ambient pH on resource-limited growth for each set of experimental conditions. An experimental program of this type would reveal the physiological role of ambient pH in the ecology of *Sphagnum*. At present we do not know if the role of reduced ambient pH is to lower the growth rate of competitors directly or if pH primarily affects resource acquisition and thus changes the kinetics of resource-limited growth for specific resources. It would be interesting to find out if particular species of *Sphagnum* grow better over a wider range of pH values and/or resource levels when they are grown monospecifically than when they are grown conspecifically. If particular species do better when grown alone, it would indicate that species segregation along a resource gradient was probably the result of competitive interactions. The data obtained from the experimental program outlined could be used in mathematical models of resource competition already developed for phytoplankton and higher plants (Kilham & Tilman, 1979; Tilman, 1982).

Traditionally, bog plants have been considered organisms that have evolved special adaptations necessary to survive in a rigorous nutrient-poor environment (Moore & Bellamy, 1974). This point of view may well be essentially correct with respect to pitcher plants and other carnivorous organisms,

but it is probably not valid for *Sphagna*. These plants are not merely existing in bogs; they are the dominant competitors. I hypothesize that they assume this role because they have metabolic control over nutrient levels and hydrogen-ion concentrations in environments having certain prerequisite hydrologic and geologic characteristics, namely, environments where cation-loading rates are minimal. Ombrotrophic bogs that receive cations primarily from atmospheric deposition are this type of environment. It has been known for some 70 years that high cation concentrations actually kill *Sphagna* (Skene, 1915), and it is likely that this occurs because high cation concentrations and/or cation loadings impede the ability of *Sphagna* to control their environments (see above). Environmental control is essential for *Sphagna* because it makes it possible for these mosses to outcompete one another and higher plants and algae for resources.

I thank Howard Crum for encouraging me to write this review. Celia A. Hooper and Susan S. Kilham critically read the manuscript and offered many helpful suggestions. I was supported by a NSF Science Faculty Professional Development Award (SPI-7914932).

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REVIEW

Plants of Essex County, a preliminary list, by Wilfred Botham. 1982. xiv + 224 pp. Essex Region Conservation Authority, 360 Fairview Ave., W., Essex, Ontario N8M 1Y6. \$8.50 (Can. funds, postpaid).

Essex County is the southernmost in Canada and contains many plant species rare or absent elsewhere. Its flora is thus of special interest to Canadians. Finally, a plant list is available for this most interesting area, including Point Pelee National Park.

The product of over 40 years of botanizing by Wilfred Botham, this is a fine piece of original work. The format is an annotated list, with scientific names, common names, and flowering times where applicable. Also, for each species, the coded distribution within the county is noted, based on areas outlined in the introduction. Literature reports are cited, and collector date, and herbarium are noted for vouchers. Unannotated lists of bryophytes and fungi are included at the end of the text.

This book should be of interest to all botanists in the western Lake Erie-Lake St. Clair regions. It is offset from typescript and has a paper cover and "perfect" binding. People using it in the field may wish to strengthen the binding.

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✓ CAREX HELEONASTES, NEW TO MICHIGAN AND
THE CONTIGUOUS UNITED STATES. //

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On June 10, 1980, D. Henson collected a somewhat immature specimen of an unusual *Carex* in Schoolcraft County, Michigan. It was apparently *Carex heleonastes* L. fil., new to the continental United States (excluding Alaska). Both of us visited the site on June 20, 1981 to secure better material and found *C. heleonastes* to be rare but widespread in open, fen-like, sedge-dominated swales in a sparse, wet, woodland of stunted *Picea mariana* with scattered *Larix laricina* and *Thuja occidentalis*. Dominating the openings were *Scirpus hudsonianus*, *Carex limosa*, *C. diandra*, *Smilacina trifolia*, and *Rubus pubescens*.

Carex heleonastes (Fig. 1) belongs to the relatively difficult section *Canescentes* (Fries) Christ. It differs from all other species of the section in eastern North America, *C. arcta*, *C. brunneus*, *C. canescens*, *C. glareosa*, *C. lachenalii*, *C. lapponica*, *C. loliacea*, *C. mackenziei*, *C. marina*, *C. tenuiflora*, *C. trisperma*, and *C. ursina*, by a combination of features: culms 15-45 cm tall, strongly scabrous below the inflorescence; inflorescences compact, mostly 15-25 mm long, with 3-6 ovoid-globose gynecandrous spikes 5-10 mm long, the lower \pm overlapping; perigynia ellipsoid, distinctly nerved, brownish, 2.5-3.5 mm long, with a short, scaberulous beak (Chater, 1980; Hudson, 1977; Hultén, 1968, Mackenzie, 1931; Toivonen, 1981).

Although circumboreal, *Carex heleonastes* is an uncommon plant in eastern North America, known from a number of stations in northernmost Ontario and adjacent Quebec, mostly near Hudson Bay. Recent extensive collecting in the Hudson's Bay lowlands, primarily by J. L. Riley (TRT) have shown that it is widespread in fens throughout the region, but it has been considered exceedingly rare, as shown in maps by Dutilly, Lepage & Duman (1954), and Hultén (1968). The record from Thunder Bay, Ontario, reported by Dutilly, Lepage & Duman and mapped by Hultén does not appear to be supported by a specimen and was rejected as unverified by Given & Soper (1981; p. 6). Ours is the first confirmed report from the Lake Superior region and adds yet another northern disjunct to the list presented in Given & Soper (1981). This find extends the range about 600 km south of the nearest colonies in the Hudson Bay lowlands and into the area covered by the standard northeastern North American floras (Fernald, 1950; Gleason, 1952; Gleason & Cronquist, 1963).

Michigan Collections: Schoolcraft Co., [ca 30 mi. NW of Manistique], June 10, 1980, Don Henson 1143 (MICH, WIS). June 20, 1981, A. A. Reznicek 6305, with S. A. Reznicek and D. Henson (MICH).

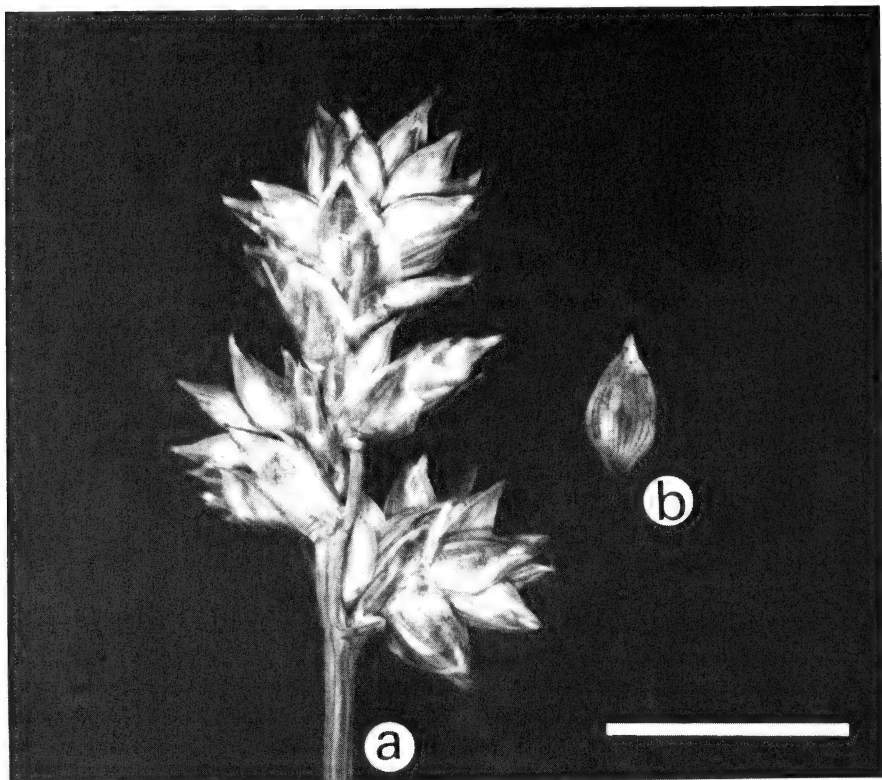


Fig. 1. *Carex heleonastes*, from Reznicek 6305; A, inflorescence; B, perigynium. Bar in figure equals 5 mm.

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n TRICHOME VARIATION AND THE ECOLOGY
OF ARCTOSTAPHYLOS IN MICHIGAN. //

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Arctostaphylos uva-ursi has been a source of taxonomic uncertainty. The most recent treatment recognized four subspecies and two varieties in North America, differing in pubescence of young stems and petioles and greatly overlapping in ranges. In Michigan the non-glandular var. *coactilis*, the most common of the entities in the state (63.6% of all randomly collected specimens), prefers the most exposed habitats with the least water-retentive substrates; the reverse is true for the glandular subsp. *adenotricha* (29.5% of specimens); and the glandular subsp. *longipilosa* (6.8% of specimens) was found only in jack pine woods. Var. *coactilis* may be insensitive to pH; subsp. *adenotricha* may prefer more basic substrates; and subsp. *longipilosa* may prefer more acidic ones. The study suggests that introgression may be the source of much of the morphological intermediacy and that the species as a whole occurs in Michigan on substrates that are more commonly neutral to basic than is widely believed.

The bearberry, *Arctostaphylos uva-ursi*, is well-known to those who have enjoyed Michigan's Great Lakes beaches and dunes or gathered blueberries in the state's jack pine woods. It is, in fact, very common on sandy and rocky sites, including beaches, dunes, and mountains, particularly throughout the northern parts of North America, Europe, and Asia. As often seems to be the case with common, widespread plants, the species has generated much taxonomic uncertainty. Numerous entities have been described at the species level and below and then variously reinterpreted by subsequent authors (Cockerell, 1889; Fernald & Macbride, 1914; Fernald, 1933; Eastwood, 1946; Hultén, 1948; Calder & Taylor, 1965, 1968; Wells, 1968; and Löve et al., 1971), but only recently have modern, biosystematic methods been employed to resolve the disagreements.

Using evidence from trichome morphology (various combinations of short *S* or long *L* hairs which are glandular + or non-glandular—on young stems and petioles), cytology ($2n=26$ and 52, with some individuals 39 and 65), and phenolic chemistry, Packer & Denford (1974) recognized four subspecies and two varieties in North America. Subsp. *longipilosa* (S+S-L-) and subsp. *stipitata* (S+S- or S+) were newly described, while subsp. *uva-ursi*, which included var. *uva-ursi* with S- hairs and var. *coactilis* Fernald & Macbride with S-L- hairs, and subsp. *adenotricha* (Fernald & Macbride) Calder & Taylor (S+S-L+L-) were maintained. This treatment serves as the nomenclatural basis for the following discussion.

Packer & Denford concluded that their study raised more questions than it answered and stated that many taxonomic, phytogeographical, and ecological problems remain. Indeed, some pubescence types remain unassigned taxonomically, and the geographic ranges given for the recognized taxa overlap to such an extent that ecological differences (habitat preferences) might be expected to exist if the taxa are, in fact, biologically meaningful. Packer & Denford pointed

out, however, that to their surprise "no detailed ecological study of this species has ever been undertaken." Even so, Wherry (1920) had reported that *A. uva-ursi* had been collected "on limestone north of Lake Superior," as well as from sandy, acidic sites, and concluded that further study of the species was desirable to ascertain "any varietal differences associated with these divergences in soil reaction."

During the summer of 1976 I characterized in some detail four rather distinct habitats in which *A. uva-ursi* occurs in northern lower Michigan. Each was described with respect to (1) certain features (such as bulk density, total porosity, field capacity, available moisture, textural class, percent organic matter, temperature, and pH) of that horizon or place in the soil (most of which are entisols, suborder psamments) in which adventitious roots of *A. uva-ursi* were most abundant, (2) the degree of exposure to sunlight, and (3) associated plant species. Analysis of the data suggested that substrate moisture, substrate pH, and exposure to sunlight were the features most likely correlated with the occurrence of the various entities throughout the remainder of the state and that associated species might provide additional evidence of any habitat preferences indicated by the physical parameters.

During the warmer months of 1978 and 1979 I collected specimens throughout a major portion of the species' range in Michigan. As I approached each population I first chose in a random fashion which individuals would be collected and incorporated in this study. The danger of favoring one taxon over another in this process is essentially non-existent due to the fact that a good hand lens is usually required for identification, and the random choices were made from a minimum distance of 10 meters.

Each site was then classified with respect to exposure. "Shaded" sites included those in relatively dense woods (such as an *Abies-Thuja* woods) or the shade on the north edge of such woods (Fig. 1) or those located directly beneath a densely-shading tree. "Intermediate" sites included those in relatively open woods (such as a jack pine woods) or on the east or west edges of woods. "Open" sites included those exposed to direct sunlight for a major portion of the time between sunup and sundown; open sites included, most typically, sand dunes and roadsides.

The substrate clinging to adventitious roots exposed by pulling up a branch of the plant to be collected was classified with respect to its estimated ability to hold water. "Wet" substrates were most commonly found, surprisingly, at rocky or gravelly sites where very rich organic material had accumulated in the interstices between rock fragments beneath the surface (Fig. 2). Less commonly wet substrates were sandy or loamy but in such cases had high levels of organic material. "Intermediate" substrates were usually sandy but were noticeably darkened with organic matter (although to a lesser extent than wet substrates), while "dry" substrates were in almost all cases sandy and with less or no organic incorporation (usually dune sand). As it turned out, most substrates were clearly assignable to one of the three classes; those which seemed borderline were classified as intermediate.

Determination of substrate pH was made in the field using material which clung to the exposed roots and a LaMotte field pH kit (Model ST-1001-T).

It was not until approximately one year after the field work had been completed that the pubescence and therefore identity of each specimen was determined. Since the collection numbers representing the plants and localities had been listed *a priori* under the appropriate site categories for exposure, substrate moisture, and substrate pH, it was possible to determine without bias the percentage each taxon constituted of the total collected from each category.

As another indication of habitat conditions, associated plant species (woody plants within about 10 meters and herbs within about five, unless they were obviously subjected to very different conditions) were recorded.



Fig. 1. Shaded site on the north edge of an *Abies-Thuja* woods. Wet limestone gravel substrate (Fig. 2). Arrow indicates location of *A. uva-ursi* (var. *coactilis* and subsp. *adenotricha*), McGulpin Point, Emmet Co. Fig. 2. Handful of substrate classified as wet found beneath an apparently dry and gravelly surface (Fig. 1) in which *A. uva-ursi* (var. *coactilis* and subsp. *adenotricha*) was extensively rooted adventitiously. McGulpin Point, Emmet Co.

In all, 132 individuals were collected in the areas shown (Fig. 3). Of these, 84 (63.6%) were assignable to subsp. *uva-ursi* var. *coactilis* (S-L-); 39 (29.54%) to subsp. *adenotricha* (S+S-L+L-); and 9 (6.8%) to subsp. *longipilosa* (S+S-L-). Five individuals collected from disturbed, roadside type habitats and assigned to subsp. *adenotricha*, however, are of a questionable nature in that there is a low percentage (5 to 25% of all hairs) of glandular hairs on four; the pubescence varies from branch to branch on two (from very glandular to very few glands); the glands are shriveled and dry (dead?) on one; and there is a small percentage (20% of all glandular hairs) of the requisite long glandular hairs on another. In addition, all nine individuals assignable to subsp. *longipilosa*, which were collected from jack pine woods, have low percentages of glandular hairs (four have the required S+ hairs only very sporadically, while the other five have 5 to 25% of all hairs S+); two are variable in pubescence from branch to branch (as above); and all nine have glands which are shriveled and dry (as above). It has also been my general observation that when glands are few they are usually short, although

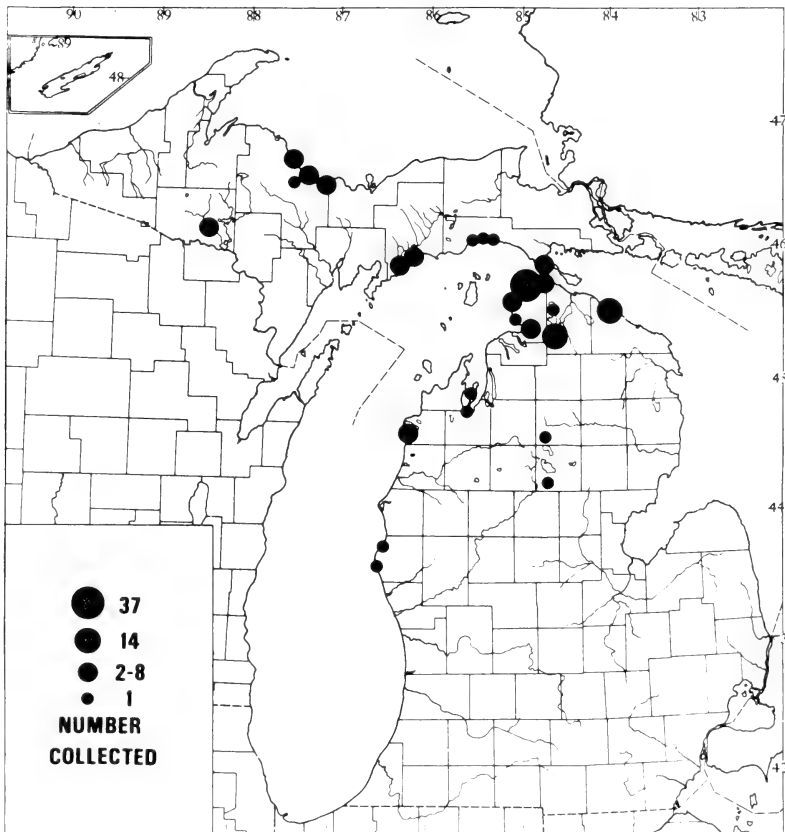


Fig. 3. Numbers of specimens collected from the areas as shown and reported herein.

the reverse is not true (as seen in subsp. *longipilosa* from the mountains of western North America).

Figure 4 indicates that var. *coactilis* makes up an increasingly large percentage of plants present as the amount of sunlight increases (for example, of 30 specimens collected from sites classified as shaded, 36.7% are assignable to var. *coactilis*; this figure is 55.7% and 95.1% from intermediate and open sites, respectively); that the reverse is true for subsp. *adenotricha*; and that subsp. *longipilosa* is only represented in sites classified as intermediate. Also apparent is the fact that var. *coactilis* is better represented in shaded places than subsp. *adenotricha* is in open ones.

Figure 5 shows that var. *coactilis* makes up an increasingly large percentage of the plants present as the ability of the substrate to hold water decreases; that the reverse is true for subsp. *adenotricha*; and that subsp. *longipilosa* is present only on substrates classified as intermediate. Again, var. *coactilis* is much more frequent on wet substrates than is *adenotricha* on dry ones (to the point where the latter is not even represented in the dry category).

Figure 6 suggests that var. *coactilis* is insensitive to substrate pH, as it makes up roughly equal percentages of the plants in each of the pH categories; that subsp. *adenotricha* makes up increasingly large percentages of the plants present as the substrate becomes more basic; and that subsp. *longipilosa* prefers the most acidic substrates.

Several other points not as apparent from examination of the figures should still be made: With regard to exposure, the 4.9% value for subsp. *adenotricha* in the open (Fig. 4) actually represents only two specimens, neither from a dry substrate. If actual numbers of specimens are considered, as opposed to percentages, approximately the same kind of information emerges concerning exposure and substrate moisture (except that the majority of specimens assignable to var. *coactilis* actually occur on substrates of intermediate moisture). With respect to substrate pH, however, actual numbers indicate that of the 117 individuals of *A. uva-ursi* for which this value was determined, only 36 (30.8%) occurred on acid substrates (pH < 6.6), while 40 (34.2%) were found on neutral sites (pH 6.6-7.3) and 41 (35%) on alkaline ones (pH > 7.3). More specifically, 50 of the 72 (69.4%) individuals of var. *coactilis*, and 31 of the 37 (83.8%) assignable to subsp. *adenotricha* occurred on neutral to basic substrates.

Table I lists those species which occurred six or more times with *A. uva-ursi*. By comparing the overall incidence of the three taxa statewide to their frequency of coexistence with the selected associates, a measure of the affinity (or lack thereof) between the former and the latter may be attained. For example, of the total of 132 specimens of *A. uva-ursi* randomly collected statewide, 63.6% were var. *coactilis*. However, of the 24 specimens of bearberries taken statewide which were associated with *Pteridium aquilinum*, 83.3% were assignable to var. *coactilis*. This would indicate that var. *coactilis*, relative to its occurrence throughout the state as a whole, occurs conspicuously more frequently with *P. aquilinum*. I have indicated with an "m" in Table I those species with which the three taxa under consideration were found "conspicuously more frequently" (arbitrarily chosen to be greater than 77% of the time the species as a whole was found with them for var. *coactilis*; greater than 44% for subsp.

adenotricha; and greater than 14% for subsp. *longipilosa*). Similarly, I have indicated with an "I" those species with which each of the three taxa occurred "conspicuously less frequently" (arbitrarily chosen to be less than 56% for var. *coactilis*; 17% for subsp. *adenotricha*; and subsp. *longipilosa* is perhaps too infrequent overall to be considered in this regard). It is interesting to note that 14 species with which var. *coactilis* was found "conspicuously more frequently" were found "conspicuously less frequently" with subsp. *adenotricha*, or vice versa, and that no species was a conspicuously more frequent or conspicuously less frequent associate of both var. *coactilis* and subsp. *adenotricha* (two observations which are hardly surprising in view of the methods involved in generating this list). Also notable is the fact that the shade "form" of *Smilacina stellata* (Voss, 1972) was found to occur only with subsp. *adenotricha*.

Several points concerning the species as a whole, as well as three of the entities recognized by Packer & Denford (1974), may be elucidated from what has been reported here. Because of the random nature of the process by which the specimens were obtained, the results probably represent fairly accurately the actual proportions of the taxa in Michigan, only one of which (var. *coactilis*) was depicted as extending into the state by Packer & Denford (1974). These plants were almost always found within a few miles of a large body of water. The temperature-moderating effects produced by lakes have undoubted significance with respect to the Michigan distribution of this boreal species.

The rather widespread impression that this species is acid-loving (Warming, 1909, p. 211; Blom, 1941; McVean, 1964; Barnes & Wagner, 1981) is most probably due to a combination of two facts. It is ericaceous and as such (Cullen, 1978, p. 125) is commonly assumed to be acidophilous, and it is perhaps best-known, at least east of the Mississippi River, from sandy substrates (which are also commonly assumed to be acidic). The fact is that in Michigan a majority of individuals (81 of 117, or 69.2%) were found on neutral to alkaline substrates, even though subsp. *longipilosa* seems to be restricted to those which are extremely to strongly acidic (pH 4.0-5.5). While this may mean that var. *coactilis* and subsp. *adenotricha* actually prefer non-acidic substrates, it is just as likely (as suggested for the former in Fig. 6) that these entities are not particularly sensitive to pH and that it just happens that the Michigan habitats most suitable (for other reasons) are neutral to basic. I have determined, in fact, that the sandy beaches and dunes bordering Lake Michigan and northern Lake Huron where this species is very abundant have pH's of about 7.0 to 8.0. This rather surprising fact is consistent with the other reports (Forsyth & Hamilton, 1974).

The results reported here tend to support several other points regarding the three infraspecific taxa under consideration. Var. *coactilis* occurs in all habitats in which the species is found but seems to prefer the most xeric ones. In fact, individuals of var. *coactilis* occurring in the most mesic habitats are quite often diffuse in form and set little fruit, while just the opposite is true of those growing on sand dunes, for example.

Subsp. *adenotricha*, on the other hand, seems to prefer shaded sites with wet substrates and is conspicuously absent from exposed, dry places. I have never observed it on a sand dune. It is interesting to note that this entity sets

TABLE I. Species occurring with *A. uva-ursi* 6 or more times. Total occurrences (Total); occurrences with each of the infraspecific taxa under consideration (No.) and percentage this number is of the total (%). C = subsp. *uva-ursi* var. *coactilis*, A = subsp. *adenotricha*, L = subsp. *longipilosa*, m = occurring conspicuously more frequently with, and l = occurring conspicuously less frequently with.

	Total	No.	C	%	No.	A	%	No.	L	%
Statewide	132	84		63.6	39		29.5	9		6.8
<i>Thuja occidentalis</i>	47	25	l	53.2	22	m	46.8	0		0
<i>Abies balsamea</i>	38	19	l	50.0	19	m	50.0	0		0
<i>Pinus strobus</i>	37	24		64.9	13		35.1	0		0
<i>Picea glauca</i>	35	15	l	42.9	20	m	57.1	0		0
<i>Pinus resinosa</i>	29	20		69.0	8		27.6	1		3.4
<i>Betula papyrifera</i>	28	19		67.9	9		32.1	0		0
<i>Juniperus communis</i>	28	19		67.9	9		32.1	0		0
<i>Pteridium aquilinum</i>	24	20	m	83.3	4	l	16.7	0		0
<i>Pinus banksiana</i>	22	13		59.1	0	l	0	9	m	40.9
<i>Vaccinium angustifolium</i>	20	16	m	80.0	0	l	0	4	m	20.0
<i>Maianthemum canadense</i>	19	13		68.4	6		31.6	0		0
<i>Shepherdia canadensis</i>	17	6	l	35.3	11	m	64.7	0		0
<i>Fragaria virginiana</i>	16	7	l	43.7	8	m	50.0	1		6.2
<i>Gaultheria procumbens</i>	15	13	m	86.7	1	l	6.6	1		6.6
<i>Cladina</i> spp.	13	8		61.5	1	l	7.7	4	m	30.8
<i>Acer rubrum</i>	9	7	m	77.8	2		22.2	0		0
<i>Juniperus horizontalis</i>	9	5	l	55.5	4	m	44.4	0		0
<i>Linnaea borealis</i>	9	4	l	44.4	5	m	55.5	0		0
<i>Prunus virginiana</i>	9	7	m	77.8	2		22.2	0		0
<i>Quercus rubra</i>	9	6		66.7	0	l	0	3	m	33.3
<i>Comptonia peregrina</i>	7	6	m	85.7	0	l	0	1	m	14.3
<i>Polygala paucifolia</i>	7	3	l	42.9	4	m	57.1	0		0
<i>Populus tremuloides</i>	6	5	m	83.3	1	l	16.7	0		0
<i>Prunus pumila</i>	6	5	m	83.3	1	l	16.7	0		0
<i>Smilacina stellata</i> : sun	6	4		66.7	2*		33.3	0		0
shade	3	0	l	0	3	m	100.0	0		0

*large portions of plants burned and dead

little fruit in Michigan, while farther north and in the Rocky Mountains it occurs more frequently in the open (albeit on moister substrates on the average), and in these places abundant fruit may be set (study in progress). It is perhaps reasonable to speculate, however, that in Michigan subsp. *adenotricha* may be restricted to the shaded, cool, wet sites (the least water-stressful to the plant) where sunlight is insufficient for abundant fruit set, while elsewhere (where edaphic and atmospheric conditions are less water-stressful) it is able to grow in the open and thus set fruit abundantly. (It is tempting to suggest that this apparent inability to set abundant fruit in Michigan is involved in restricting further migration.)

The habitat preferences discussed above are well supported by consideration of associated species. For the most part, plants better known from drier habitats were more frequently associated with var. *coactilis* (*Pteridium aquilinum*, *Vaccinium angustifolium*, *Gaultheria procumbens*, *Acer rubrum*, *Prunus*

virginiana, *Comptonia peregrina*, *Populus tremuloides*, and *Prunus pumila* were found conspicuously more frequently with var. *coactilis*), while those species characteristic of more mesic habitats were more frequently found with subsp. *adenotricha* (*Thuja occidentalis*, *Abies balsamea*, *Picea glauca*, *Shepherdia canadensis*, *Fragaria virginiana*, *Juniperus horizontalis*, *Linnaea borealis*, and *Polygala paucifolia* were found conspicuously more frequently with subsp. *adenotricha*). Since all nine specimens of subsp. *longipilosa* were obtained from jack pine woods, it is hardly surprising that it was frequently found with species which often occur in such habitats (*Pinus banksiana*, *Vaccinium angustifolium*, *Cladina* spp., *Quercus rubra*, and *Comptonia peregrina* were found conspicuously more frequently with subsp. *longipilosa*). Conclusions and speculation regarding subsp. *longipilosa* are more hazardous, in part due to the small number of specimens involved, but it seems that some significance can be attached to the fact that it was only obtained from jack pine woods. A consideration of the possible role played by hybridization might lead to a better understanding of this entity, as well as the five individuals of questionable nature assigned to subsp. *adenotricha* and the species as a whole.

Several authors (Raup, 1947; Packer, 1967; Calder & Taylor, 1968; Hultén, 1971; Löve et al., 1971; Packer & Denford, 1974) have made reference to the great frequency of plants which are variously intermediate, and some have suggested that introgression may be involved. Certainly the chromosome numbers $2n=39$ and 65 suggest hybridization, most likely (unless unreduced gametes are involved) between individuals with 26 and 52 somatic chromosomes in the first case and between plants with $2n=52$ and 78 (Rosatti, 1981) in the latter. The results of progeny tests (ms. in preparation) in which approximately 300 individuals grown from seeds from known maternal parents were examined also indicate that hybridization takes place. Finally, 14 individuals in the present study possess characteristics which suggest that they are of hybrid origin. Specimens assigned to subsp. *adenotricha* appear to have resulted from introgression with non-glandular plants in that they have a rather suspiciously low percentage of glandular hairs, which are often shriveled and dry. The fact that they were collected from disturbed habitats and that the expression of the genome (variable pubescence) is often inconsistent throughout each plant also implies that they are hybrid in origin.

Individuals assigned to subsp. *longipilosa* also have low percentages of the requisite (S+) glandular hairs; glands which are shriveled and dry; and variable pubescence. The fact that each was collected from a jack pine woods, another kind of disturbed habitat (by fire), is also interesting. Whether these plants are of hybrid origin and are therefore best equipped genetically to survive in such a "hybrid habitat" (Anderson, 1949), is currently under investigation. Although the jack pine sites were classified as intermediate with respect to exposure and substrate moisture (and thus could be considered "hybrid habitats"), the associated species which occur conspicuously more frequently with subsp. *longipilosa* are usually known from rather xeric habitats,¹ and the pH's (less than

¹These jack pine forests are, apparently, quite xeric. Depth to water table, an important variable not determined in this study, is probably greater there than for most other sites, which are much closer to one of the Great Lakes. This depth could be so great as to nullify the water holding abilities of the substrates. These jack pine sites are also much less temperature-moderated by the Great Lakes than most of the other sites.

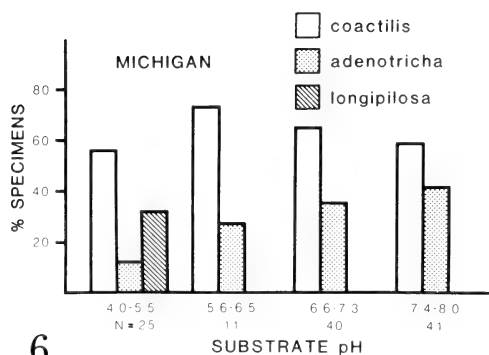
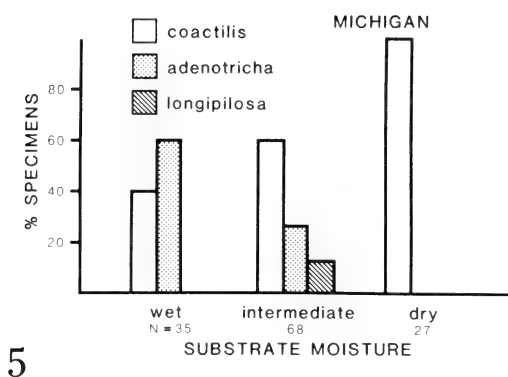
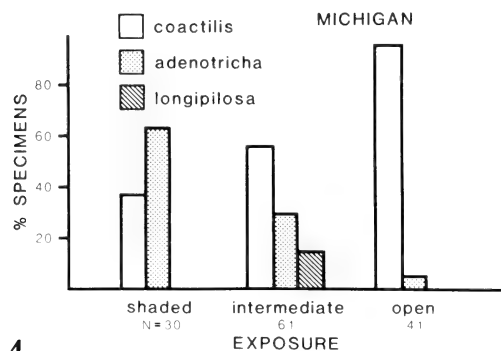


Fig. 4-6. Comparisons related to exposure, substrate moisture, and substrate pH4. Percentages of specimens of *A. uva-ursi* collected from shaded sites (30 specimens), intermediate (61 specimens), and open (41 specimens) and assigned to infraspecific taxa found in Michigan. 5. Percentages of specimens of *A. uva-ursi* collected from wet substrates (35 specimens), intermediate (68 specimens), and dry (27 specimens) and assigned to infraspecific taxa found in Michigan. 6. Percentages of specimens of *A. uva-ursi* collected from substrates which were strongly to extremely acidic (pH less than 5.6, 25 specimens), slightly to moderately acidic (pH 5.6-6.5, 11 specimens), neutral (pH 6.6-7.3, 40 specimens), and mildly to moderately alkaline (pH 7.4-8.0, 41 specimens) and assigned to infraspecific taxa found in Michigan.

5.6) are certainly not intermediate. Another possibility is that these plants assigned to subsp. *longipilosa* are genetically (i.e., in reality) subsp. *adenotricha* but modified because the environment is drier or more acidic (or both) than that to which they are best adapted (plants assignable to subsp. *adenotricha* were never observed to occur in a jack pine woods).

I am grateful to Dr. E. G. Voss for introducing me to the problem and helping me, especially during early stages of the research at the University of Michigan Biological Station, and also to Drs. B. V. Barnes and W. H. Wagner for helpful criticisms and David Bay for photographic assistance.

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245 STUDIES ON MICHIGAN CHRYSOPHYCEAE. V. 5-14

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Since Wujek and co-workers published records of Chrysophyceae from Michigan (1972, 1973, 1975, 1977), additional samples have revealed five other species new to the state, two of them new to the continental United States (marked with an asterisk below), and ten new localities for members of the Synuraceae previously recorded from the state. All species reported here or cited from the literature were observed with EM. Methods of collection and light and electron microscopy are as described in the papers cited above, except that some observations were made with a Hitachi H-11 TEM.

New locality records include *Mallomonas papillosa*, *M. striata*, and *Synura echinulata* from Smith's Bog (Cheboygan Co.), *Mallomonas caudata*, *M. crassisquama*, *M. tonsurata*, *Spiniferomonas trioralis*, and *Chrysosphaerella coronacircumspina* from Douglas Lake (Cheboygan Co.), *Paraphysomonas vestita* from Tittabawassee River (Midland Co.), and *Mallomonas heterospina* from Saginaw River (Bay Co.).

**Mallomonas corymbosa* Asmund & Hilliard (Fig. 1).

This species, first observed in material from Alaska (Asmund & Hilliard, 1961), has been subsequently reported from Alaska (Asmund & Takahashi, 1969) and also from Canada (Kristiansen, 1975) and Bangladesh (Takahashi & Hayakawa, 1979). We observed it from a plankton tow taken in a ditch immediately south of Mt. Pleasant (Isabella Co.).

Mallomonas multiunca Asmund (Fig. 2).

Recently reported from continental United States (Wujek et al., 1981), it was originally described from material collected in Denmark (Asmund, 1956). It has been observed from Rumania (Peterfi, 1974), the Netherlands (Wujek & van der Veer, 1976), and several more times from Denmark (Asmund, 1959; Kristiansen, 1976; Zimmerman, 1977). Although not specified in their papers, the electron micrographs published by Harris & Bradley (1957, 1960) presumably came from English specimens. Our observations are from Smith's Bog (Cheboygan Co.).

**Mallomonas pugio* Bradley (Fig. 3).

Since its description from Iceland collections (Bradley, 1964), this species has been reported from Greenland (Nygaard, 1978) and Russia (Balonov, 1978). It was found in Smith's Bog (Cheboygan Co.).

Mallomonas teilingii Conrad (Fig. 4).

Scales of this species were first reported from Denmark on the basis of EM by Asmund (1956). Further reports from Rumania (Peterfi, 1966), Denmark (Kristiansen,

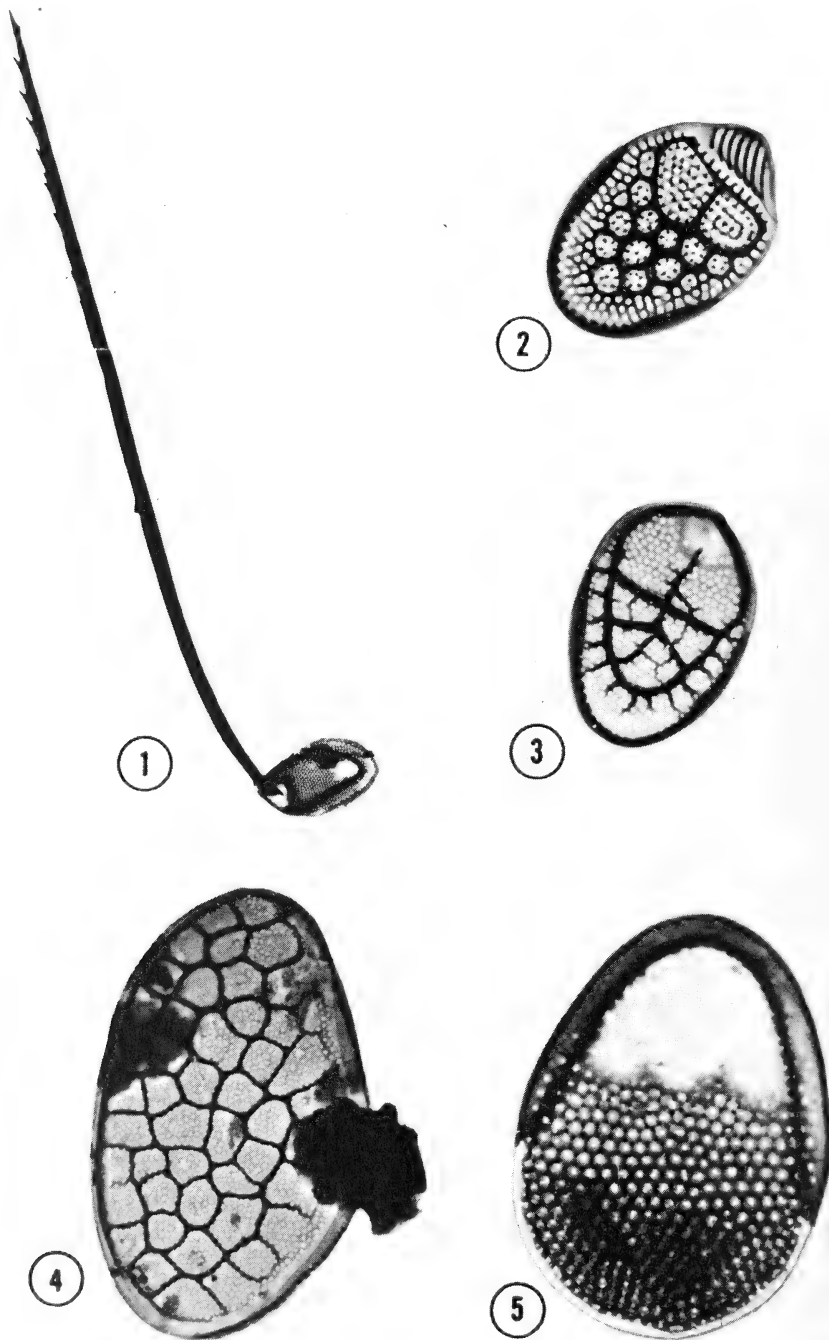


Fig. 1. *Mallomonas corymbosa*, $\times 3,200$. Fig. 2. *M. multiunca*, $\times 10,000$. Fig. 3. *M. pugio*, $\times 10,000$. Fig. 4. *M. teilingii*, $\times 8,100$. Fig. 5. *Mallomonopsis elliptica*, $\times 10,000$.

1976), Iowa (Wee et al., 1976), and Sweden (Cronberg, 1980a) have shown it to be both distinctive and cosmopolitan. Scales occurred in samples from the Saginaw River at Bay City (Bay Co.).

Mallomonopsis elliptica Matv. (Fig. 5)

This taxon is reported more often than any other in the genus. In addition to previous records from Europe, North America, Asia, and Africa (Wujek & Timpano, 1982), this taxon has also been reported from Canada (de Puytorac et al., 1972) and Sweden (Cronberg, 1980b). The scale illustrated here appeared in samples from Smith's Bog (Cheboygan Co.).

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A QUANTITATIVE STUDY OF THE FLORA OF
ABANDONED LEAD-ZINC MINES IN
SOUTHWESTERN WISCONSIN

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The landscape of the Upper Midwest is a mosaic of diminishing native plant communities and ecosystems dominated by human activity. In addition to new vegetation types contrived for agriculture and urbanization, industrial wastelands are created where the processes of vegetation recovery are impeded by the harshness of the site. The disturbance of native vegetation is nowhere more complete than on mined land where the soil itself is buried beneath tons of mine waste. If stable vegetation could be established on the waste, many of the environmental problems it creates could be alleviated.

The appearance of these new substrates poses a challenge both to the "restoration ecologist" and to the local flora. Without further human intervention, the slow processes of colonization will result in a new assemblage of species uniquely adapted to the site. As restoration of vegetation requires close simulation of natural processes, considerable ecological information can be derived from monitoring the patterns of natural revegetation.

Factors impeding colonization include low water-holding capacity of waste, physical instability of waste bed surface, nutrient deficiency, temperature extremes, extreme pH, and lack of propagule source. The process of natural revegetation is further limited when toxic substances are present in the waste material. The work of Bradshaw et al. (1965) and others on colonization of derelict heavy metal mines has demonstrated that potential colonists must undergo selection for tolerance of both toxic heavy metals and a harsh environment. So strong are the selective pressures of these sites that "it appears that species that occupy toxic metal contaminated habitats only do so because they evolve tolerance" (Bradshaw 1975). The resulting communities are unique species-assemblages composed of populations of tolerant individuals.

A quantitative survey of the flora of heavy-metal mines in southwestern Wisconsin was conducted. The Wisconsin lead district has one of the longest records (~1800-1979) of continuous ore production in the United States (Heyl et al. 1959). More than 2000 small mines and associated waste dumps are scattered throughout the district.

The research area lies within the Upper Mississippi Zinc-Lead district which includes southwestern Wisconsin, the northwest corner of Illinois, and a narrow band of eastern Iowa. In Wisconsin, the district is located in the unglaciated Driftless Area on Ordovician bedrock of Galena and Platteville dolomites overlying St. Peter Sandstone. The dominant topographic feature is a maturely dissected upland sloping gently to the south (Heyl et al. 1959). Pre-settlement vegetation was a mixture of oak forest, oak savanna, and tall grass

prairie on deep, silt loam soils. Most of the region is now under cultivation. Zinc ores are primarily sphalerite (ZnS) and smithsonite (ZnCO_3). Galena (PbS) is the principal lead ore.

The earliest mines were small-scale surface excavations known as "diggings." Ore deposits were removed with hand tools creating pits often 3 m in diameter and 2 m deep. Waste rock was heaped around the pits and scattered between them. The Badger Diggings site included in this study represents such an excavation. Later, ores were removed by underground mining using the random room-and-pillar method. Crushed ore was then concentrated by gravity concentration (jig milling). Waste material (jig tailings) is deposited over the original topsoil to depths of several meters. The tailings are a nutrient-poor mixture of coarse dolomitic gravel- and sand-size material containing elevated levels of zinc and lead. Physical characteristics of the tailings have been described by Cashell (1980).

Few of the mines scattered throughout the district have been undisturbed since abandonment. Of these, 11 were selected for study (Table 1). An attempt was made to locate sites representing a diversity of ages. Replicate sites of similar ages were included when possible. With the exception of the "Badger Diggings," site selection was made on the basis of verifiable date of abandonment; lack of disturbance since abandonment; and similarity of tailings, slope, aspect, and adjacent vegetation. Unless otherwise noted, all sites are located in Lafayette

TABLE 1. Location and date of abandonment of 11 study sites.

	Date of Abandonment	Location
Badger Diggings	1860	N $\frac{1}{2}$ NE $\frac{1}{4}$, sec. 30 T.1N., R.1E.
Badger Mine	1900	N $\frac{1}{2}$ NE $\frac{1}{4}$, sec. 30 T.1N., R.1E.
Rowley Mine	1908	S $\frac{1}{2}$ NW $\frac{1}{4}$, sec. 33 T.1N., R.1E.
Fox Mine	1917	SW $\frac{1}{4}$ SW $\frac{1}{4}$, sec. 21 T.1N., R.1E.
Old Winskell Mine	1917	SE $\frac{1}{4}$ NW $\frac{1}{4}$, sec. 19 T.1N., R.2E.
Booty	1928	SW $\frac{1}{4}$ NW $\frac{1}{4}$, sec. 19 T.1N., R.2E.
Middie Mine	1928	SW $\frac{1}{4}$, sec. 8 T.1N., R.1E.
Thompson Mine	1945	SW $\frac{1}{4}$ NW $\frac{1}{4}$, sec. 30 T.1N., R.2E.
Pittsburgh-Benton Mine	1946	SW $\frac{1}{4}$ SE $\frac{1}{4}$, sec. 2 T.1N., R.1E.
Bautsch Mine	1964	S $\frac{1}{2}$, sec. 10, N $\frac{1}{2}$, sec. 15 T.27N., R.1E. Jo Daviess Co., Illinois.
Gensler Mine	1971	N $\frac{1}{2}$, sec. 27 T.1N., R.2E.

County, Wisconsin, on north-facing slopes of approximately 8%. All are bordered by both woodland and agricultural land.

The vegetation was sampled in June-August 1980 using 1 m² quadrats distributed in a stratified random design. Each site was divided into a sampling grid of 10 × 10 m units. One quadrat was randomly located in each grid unit. Presence of all species in the quadrat was recorded, and absolute frequency of occurrence was computed. An average of 180 quadrats per site was sampled. Vouchers are deposited in the University of Wisconsin (Madison) Herbarium (WIS).

DISCUSSION

The data (Table 2) suggest that a wide variety of species is capable of colonizing metal-contaminated mine waste but that the process is extremely slow. Even 16 years after abandonment, the vegetation of the Bautsch mine consists of 1 small clump of *Setaria viridis* (foxtail). The diversity and abundance (expressed as frequency) of vegetation tend to increase slowly; even the oldest mines contain large areas completely devoid of vegetation. The selective pressures imposed by such a harsh site dictate that the plants which persist there must be tolerant of a highly disturbed, inhospitable environment. The high frequency of several species using the C₄ photosynthetic pathway reflects the hot, dry nature of the site.

The flora is composed primarily of native species (64%), many of which are characteristic of disturbed sites. *Ambrosia artemisiifolia* (ragweed) and *Carex brevior* have been particularly successful in colonizing the mine waste. *Poa compressa* (bluegrass) and *Agrostis gigantea* (red top), the most frequent grasses, may form dense swards intermingled with clumps of *Equisetum arvense* (horsetail), *Potentilla intermedia* (cinquefoil), and *Melilotus alba* (sweet clover). Also abundant are prostrate, creeping species, such as *Euphorbia supina* (milkwort) and *Cerastium vulgatum* (mouse-ear chickweed), which form extensive mats on the tailings surface. The species number at several of the sites is surprisingly high (Table 2), owing in large part to scattered individuals of prairie species, including *Asclepias verticillata*, *Bouteloua curtipendula*, *Andropogon scoparius*, and *Solidago* spp. as well as several species uncommon in southern Wisconsin, such as *Spiranthes cernua* and *Plantago aristata*.

Species composition is remarkably similar in all the mines examined. No clear successional trend in species presence can be discerned. The percent cover by herbaceous vegetation, however, exhibits a gradual increase with successional time (Table 2). Importance of woody vegetation also increases and causes an eventual decline in herbaceous cover due to heavy shading. Vegetation dynamics at these sites is discussed at length in Kimmerer (1982, in prep.).

As mining and the need for reclamation increase, the study of such "naturally reclaimed" areas increases in importance. Undisturbed mine sites provide an excellent "natural experiment" for examining the patterns and processes of community recovery. Monitoring the progress of natural revegetation provides insight useful in ecologically sound planning for reclamation using native Wisconsin species.

TABLE 2. Frequency (%) of occurrence of species colonizing abandoned lead-zinc mines. (N = Native, E = Exotic, A = Annual, B = Biennial, P = Perennial. C₄ = using C₄ photosynthesis.)

	Badger		Rowley		Fox		Old		Pittsburg-		Thompson		Bautsch		Gensler		Notes
	Diggings	Mine	Mine	Mine	Mine	Mine	Winskell	Booty	Middle	Benton	Mine	Mine	Mine	Mine	Mine	Mine	
% cover	41.5	75.7	48.9	45.5	42.4	46.2	34.1	21.1	48.3	0.0	0.0						
# of species	25	41	42	109	47	46	74	51	78	1	29						
<i>Equisetum arvense</i>	35.5	0.0	0.0	1.2	5.4	1.6	1.1	4.8	45.9	0.0	2.9					N	P
<i>Juniperus virginiana</i>	0.0	1.4	3.8	3.7	0.0	0.0	0.6	0.0	0.0	0.0	0.0					N	P
<i>Bromus inermis</i>	0.0	58.3	0.0	0.0	0.9	11.7	0.0	0.0	8.3	0.0	0.0					E	P
<i>Poa compressa</i>	0.0	25.0	3.8	15.5	20.5	44.5	9.3	0.0	11.1	0.0	0.0					E	P
<i>P. pratensis</i>	0.0	0.0	0.0	0.0	0.0	0.0	4.5	0.6	16.7	0.0	0.0					E	P
<i>Hordeum jubatum</i>	0.0	0.0	0.0	*	0.0	0.0	*	0.0	0.0	0.0	0.0					E	A/B
<i>Agropyron repens</i>	0.0	0.0	0.0	0.0	13.4	0.8	8.9	4.2	0.0	0.0	0.0					E	P
<i>Sphenopholis intermedia</i>	0.0	0.0	0.0	*	0.0	0.0	0.0	0.0	*	0.0	0.0					N	P
<i>Agrostis gigantea</i>	0.0	0.0	0.0	1.2	35.7	2.3	36.9	47.2	18.9	0.0	10.0					E	P
<i>A. scabra</i>	0.0	0.0	0.0	2.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0					E	P
<i>Phleum pratense</i>	0.0	*	0.0	0.0	0.0	0.0	0.0	*	0.0	0.0	*					E	P
<i>Muhlenbergia sylvatica</i>	0.0	4.2	0.0	4.4	0.0	2.3	1.3	0.0	0.4	0.0	0.0					N	P
<i>M. schreberi</i>	0.0	0.0	19.2	15.5	0.0	3.1	0.0	0.0	0.0	0.0	0.0					N	P
<i>Aristida oligantha</i>	0.0	0.0	0.0	*	0.0	0.0	0.0	0.0	0.0	0.0	0.0					N	A
<i>Bouteloua curtipendula</i>	0.0	0.0	0.0	*	0.0	0.0	0.0	0.0	0.0	0.0	0.0					N	P
<i>Panicum virgatum</i>	0.0	0.0	0.0	*	0.0	0.0	0.0	0.0	*	0.0	0.0					N	P
<i>P. capillare</i>	0.0	0.0	0.0	9.9	0.9	2.3	0.0	0.0	0.0	0.0	11.4					E	A
<i>P. implicatum</i>	0.0	0.0	0.0	34.8	0.0	1.6	0.6	0.0	1.5	0.0	0.0					N	P
<i>Setaria verticillata</i>	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	4.3					E	A
<i>S. lutescens</i>	0.0	0.0	0.0	*	0.0	0.0	0.0	0.0	0.0	0.0	0.0					E	A
<i>S. viridis</i>	0.0	0.0	0.0	*	0.0	0.0	*	0.0	0.0	0.0	0.0					E	A
<i>Andropogon scoparius</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	*	0.0	0.0	0.0					N	P
<i>Carex annectens</i>	0.0	0.0	0.0	0.6	8.0	0.0	1.1	8.9	13.5	0.0	1.4					N	P
<i>C. blanda</i>	0.7	0.7	0.0	13.0	6.3	3.1	0.2	1.8	0.2	0.0	0.0					N	P
<i>C. brevior</i>	0.0	2.8	3.4	31.1	42.9	53.9	9.3	8.9	42.6	0.0	1.4					N	P
<i>C. cephalophora</i>	0.0	0.0	0.0	*	0.0	0.0	0.0	0.0	*	0.0	0.0					N	P

TABLE 2. Continued

	Badger Diggings	Badger Mine	Rowley Mine	Fox Mine	Old Winskell Mine	Booby Mine	Middle Mine	Pittsburg- Benton Mine	Thompson Mine	Bautsch Mine	Gensler Mine	Notes
Potentilla intermedia	0.0	0.0	0.0	5.6	18.8	23.4	10.4	1.2	3.0	0.0	1.4	E P
P. recta	0.0	0.0	0.0	*	0.0	*	0.0	*	0.0	0.0	0.0	E P
Geum canadensis	0.0	1.4	0.0	*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	N P
Agrimonia sp.	0.0	0.0	0.0	0.0	*	*	0.0	0.0	0.0	0.0	0.0	P
Rosa multiflora	0.0	0.0	0.0	*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	E P
Rubus cuneifolius	2.6	8.3	71.1	4.4	2.7	4.7	2.1	1.2	0.9	0.0	0.0	N P
Prunus americana	5.2	4.2	3.8	0.0	0.0	0.0	1.1	0.0	0.7	0.0	0.0	N P
P. serotina	23.3	43.1	19.2	1.2	0.9	3.9	8.3	0.0	2.4	0.0	0.0	N P
Trifolium repens	2.6	8.3	0.0	0.0	5.4	2.3	7.4	0.6	1.1	0.0	0.0	E P
T. pratense	0.0	0.0	3.8	6.2	0.0	0.0	1.5	0.0	0.0	0.0	0.0	E B
Melilotus alba	0.0	41.7	0.0	18.0	0.0	10.2	38.6	0.0	5.0	0.0	20.0	E A/B
M. officinalis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	*	0.0	0.0	E A/B
Medicago lupulina	0.0	0.0	0.0	*	1.8	7.0	0.4	0.6	0.2	0.0	1.4	E A
M. sativa	0.0	0.0	0.0	*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	E P
Desmodium illinoensis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	*	0.0	0.0	N P
Oxalis stricta	0.0	1.4	3.8	2.5	0.9	1.6	0.0	0.0	0.0	0.0	4.3	N P
Acalypha rhomboidea	0.0	0.0	0.0	12.4	3.6	0.8	0.0	0.0	0.0	0.0	1.4	N A
Euphorbia supina	0.0	0.0	0.0	32.3	1.8	5.4	3.4	1.2	7.0	0.0	1.4	N A
E. maculata	0.0	0.0	3.8	16.2	0.0	0.0	*	0.0	0.0	0.0	0.0	N A
E. nutans	0.0	0.0	0.0	*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	N A
E. corollata	0.0	0.0	*	*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	N P
Rhus glabra	0.0	0.0	21.1	0.0	0.0	0.0	1.5	0.0	0.0	0.0	0.0	N P
Acer negundo	2.6	18.1	3.8	3.7	1.8	2.3	2.8	6.6	0.7	0.0	5.7	N P
Ceanothus americanus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	*	0.0	0.0	N P
Vitis sp.	42.1	0.0	3.8	0.0	0.9	0.0	2.5	0.0	0.9	0.0	2.9	N P
Parthenocissus quinquefolia	30.9	0.0	13.4	0.0	0.0	0.0	0.9	0.0	0.7	0.0	4.3	N P
Tilia americana	0.0	0.0	*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	N P
Hypericum perforatum	0.7	0.0	0.0	67.1	5.4	18.0	2.5	0.0	0.0	0.0	0.0	E P
Viola sp.	*	0.0	0.0	*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	N P

TABLE 2. Continued

	Badger Diggings	Badger Mine	Rowley Mine	Fox Mine	Old		Winskill Mine	Booty Mine	Middle Mine	Pittsburg-		Thompson Mine	Bautsch Mine	Gensler Mine	Notes
					Mine	Mine				Mine	Mine				
<i>Lobelia spicata</i>	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0	0.8	0.0	0.0	*	0.0	0.0	N A
<i>L. inflata</i>	0.0	0.0	0.0	*	*	0.0	*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	N A
<i>Eupatorium altissimum</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	*	0.0	0.0	*	0.0	0.0	N P
<i>Kuhnia eupatorioides</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	*	0.0	0.0	*	0.0	0.0	N P
<i>Solidago</i> spp.	0.0	11.1	13.5	5.0	0.9	0.9	0.9	3.1	7.8	4.2	4.2	2.2	0.0	0.0	N P
<i>S. altissima</i>	0.0	0.0	0.0	*	0.0	0.0	0.0	0.0	*	0.0	0.0	*	0.0	0.0	N P
<i>S. nemoralis</i>	0.0	0.0	0.0	*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	*	0.0	0.0	N P
<i>S. ulmifolia</i>	0.0	0.0	0.0	*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	N P
<i>S. canadensis</i>	0.0	0.0	0.0	*	0.0	0.0	0.0	0.0	*	0.0	0.0	0.0	0.0	0.0	N P
<i>Aster pilosus</i>	0.0	0.0	0.0	10.6	7.1	7.1	7.1	4.7	0.4	0.0	0.0	0.2	0.0	18.6	N P
<i>A. ericoides</i>	0.0	0.0	*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	N P
<i>A. novae-angliae</i>	0.0	0.0	0.0	*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	N P
<i>Erigeron annuus</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	*	N A
<i>E. strigosus</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	*	0.0	0.0	0.0	0.0	N P
<i>Antennaria neodioica</i>	0.0	0.0	0.0	1.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	N P
<i>Ambrosia artemisiifolia</i>	0.0	15.3	19.2	60.9	86.6	86.6	86.6	70.3	29.9	45.8	45.8	46.7	0.0	8.6	N A
<i>Rudbeckia hirta</i>	0.0	0.0	0.0	*	0.0	0.0	0.0	0.0	*	0.0	0.0	*	0.0	0.0	N P
<i>Senecio pauperculus</i>	0.0	0.0	0.0	*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	N P
<i>Taraxacum officinale</i>	0.0	8.3	0.0	1.9	1.8	1.8	1.8	0.8	3.0	0.0	0.0	0.0	0.0	1.4	E A
<i>Lactuca canadensis</i>	0.0	2.9	1.9	3.7	0.9	0.9	0.9	0.0	4.5	1.2	1.2	0.4	0.0	0.3	N B
<i>L. scariola</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	*	0.0	0.0	0.0	0.0	0.0	E A/B
<i>Hieracium kalmii</i>	0.0	0.0	0.0	*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	N P
<i>Achillea millefolium</i>	0.0	9.7	9.6	8.1	15.2	15.2	15.2	0.8	15.9	8.3	8.3	6.5	0.0	0.0	E P
<i>A. lanulosa</i>	0.0	0.0	0.0	*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	*	0.0	0.0	N P

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THE HAMPTON CREEK WETLAND COMPLEX IN SOUTHWESTERN MICHIGAN V. SPECIES OF VASCULAR PLANTS

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The description and classification of an interesting rare and threatened plant site, the Hampton Creek wetland complex in Kalamazoo County, Michigan (Sytsma & Pippen, 1981a, b), and a successional analysis of its peatlands (Sytsma & Pippen, 1982a, b), were recently presented. Listing the vascular plant species completes the documentation of the flora.

Most voucher specimens were collected from March 1977 to October 1978 and deposited in the Hanes Herbarium of Western Michigan University. Specimens collected prior to the study period were verified. Color prints made from Kodachrome transparencies were used instead of voucher specimens for a few species either threatened or represented in the study area by few individuals.

Nomenclature is from the following sources, with some exceptions: Pteridophyte families—Crabbe, Jermy & Mickel (1975); pteridophytes and dicotyledons—Gleason & Cronquist (1963); gymnosperms and monocotyledons—Voss (1972). Common names, where applicable, were obtained from Hanes & Hanes (1947) and Voss (1972).

Community types and subtypes (Sytsma & Pippen, 1981b) are indicated by code:

Emergent Aquatic		Southern Shrub-Carr	
<i>Nasturtium-Veronica</i> subtype	EA1	<i>Cornus</i> subtype	SC1
<i>Typha-Iris</i> subtype	EA2	<i>Betula-Potentilla</i> subtype	SC2
<i>Typha-Scirpus</i> subtype	EA3	<i>Toxicodendron-Osmunda</i>	
Southern Sedge Meadow	SM	subtype	SC3
Fen	FN	Wet Northern Forest	WF
Wet-Mesic Prairie	WMP	Wet-Mesic Southern Hardwoods	WMH

Species included on the tentative list of endangered, threatened, and rare vascular plants in Michigan (Wagner et al., 1977) are preceded by asterisks.

The flora includes 77 families, 210 genera, and 369 species. The largest families are the Asteraceae with 20 genera and 44 species, the Cyperaceae with seven genera and 38 species, and the Poaceae with 21 genera and 35 species. The largest genus represented is *Carex* with 24 species.

PTERIDOPHYTES

Aspleniaceae

- Asplenium platyneuron* (L.) Oakes Ebony Spleenwort (WMH, SC3)
- Athyrium filix-femina* (L.) Roth Lady Fern (WMH, SM)
- Dryopteris austriaca* (Jacq.) Woynar Spinulose Shield-fern (SC2, WF)
- D. clintoniana* (D. C. Eat.) Dowell Clinton's Fern (WF)
- D. cristata* (L.) Gray Crested Shield-fern (WF)

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- D. spinulosa* (Mull.) Fiori Toothed Wood Fern (WF)
Onoclea sensibilis L. Sensitive Fern (SM, FN, SC3, WF)

Dennstaedtiaceae

- Peridium aquilinum* (L.) Kuhn Bracken (SM, WMP)

Equisetaceae

- Equisetum arvense* L. Field Horsetail (SM)
E. fluviatile L. Swamp Horsetail (SM)
E. hyemale L. Tall Scouring Rush (SM)
E. laevigatum A. Br. Smooth Scouring Rush (SM)

Lycopodiaceae

- Lycopodium flabelliforme* (Fern.) Blanch. Running Pine (SC3, WMH)
L. lucidulum Michx. Shining Club Moss (WF)
L. obscurum L. Ground Pine (SC3)

Ophioglossaceae

- Botrychium dissectum* Spreng. Cut-leaved Grape Fern (WF)
B. multifidum (Gmel.) Rupr. Leather Grape Fern (WF)
B. virginianum (L.) Sw. Rattlesnake Fern (WF)

Osmundaceae

- Osmunda cinnamomea* L. Cinnamon Fern (SC3, WMH, SM, FN)
O. regalis L. Royal Fern (SM, SC3, FN)

Schizaeaceae

- **Lygodium palmatum* (Bernh.) Sw. Climbing Fern (SC3)

Selaginellaceae

- Selaginella apoda* (L.) Spring Creeping Selaginella (SC1, WF)

Thelypteridaceae

- Thelypteris palustris* Schott Marsh Fern (SM, FN, EA3, WF)

GYMNOSPERMS

Cupressaceae

- Juniperus virginiana* L. Red-Cedar (SM)
Thuja occidentalis L. White-Cedar (SC3—escaped ornamental)

Pinaceae

- Larix laricina* (Du Roi) Koch Tamarack (WF, FN, SM, EA3)
Pinus strobus L. White Pine (WMH, SC3)

MONOCOTYLEDONS

Amaryllidaceae

- Hypoxis hirsuta* (L.) Cov. Yellow Star Grass (FN, SM)

Araceae

- Arisaema triphyllum* (L.) Schott Jack-in-the-pulpit (WF, WMH, SC1)
Symplocarpus foetidus (L.) Nutt. Skunk Cabbage (WF, SM)

Commelinaceae

- Tradescantia ohiensis* Raf. Glaucous Spiderwort (SM, WMP)

Cyperaceae

- Carex annectens* (Bickn.) Bickn. Sedge (SM)
C. aquatilis Wahl. (SM, FN, EA3, EA1)
C. atlantica Bailey (SM)
C. bebbii (Bailey) Fern. (SM)
C. blanda Dewey (WMH)
C. buxbaumii Wahl. (SM, FN)
C. communis Bailey (WF)
C. hystericina Willd. (SM, EA3, EA1, FN)
C. interior Bailey (SM, EA1, WF, FN)
C. lacustris Willd. (WMH, SM, SC1)
C. laevivaginata (Kuek.) Mack. (SM, WF)
C. lanuginosa Michx. (SM)
C. lasiocarpa Ehrh. (SM, FN)

- C. leptalea* Wahl. (WF, FN, EA3)
- C. normalis* Mack. (SM)
- C. pennsylvanica* Lam. (SM, WMH, SC3)
- C. prairiea* Dewey (FN, EA3, SM)
- C. rosea* Schk. (SC3)
- C. scoparia* Willd. (SM)
- C. stipata* Willd. (SM, WF)
- C. stricta* Lam. (SM, FN, EA3, EA1)
- C. swanii* (Fern.) Mack. (SM)
- C. tetanica* Schk. (SM)
- C. vulpinoidea* Michx. (SM)
- Cladium mariscoides* (Muhl.) Torr. Twig-rush (EA3, FN)
- Cyperus rivularis* Kunth Nut-grass (EA1)
- C. strigosus* L. Nut-grass (EA1)
- Dulichium arundinaceum* (L.) Britt. Three-way Sedge (FN)
- Eleocharis elliptica* Kunth (EA3)
- E. erythropoda* Steud. (EA3, EA1, SM, FN)
- E. smallii* Britt. (EA1)
- Eriophorum viridi-carinatum* (Engelm.) Fern. (FN)
- Scirpus acutus* Bigel. Hardstem Bulrush (EA3, FN, SM)
- S. americanus* Pers. Three-square (SM)
- S. atrovirens* Willd. Dark-green Bulrush (SM, EA1, EA2)
- S. cyperinus* (L.) Kunth Wool-grass (SM)
- S. expansus* Fern. Bulrush (EA1)
- S. validus* Vahl Softstem Bulrush (SM)

Iridaceae

- Iris virginica* L. Blue Flag (EA2, SM, FN, EA3, SC1, SC2)

Juncaceae

- Juncus acuminatus* Michx. Rush (EA1)
- J. brachycephalus* (Engelm.) Buch. Rush (EA1, FN, EA3)
- J. canadensis* La Harpe Rush (SM)
- J. dudleyi* Wieg. Rush (SM)
- J. effusus* L. Rush (SM, EA1)
- J. nodosus* L. Rush (EA1, FN)
- Luzula multiflora* (Retz.) Lej. Wood Rush (SM, WMH, SC3)

Juncaginaceae

- Triglochin palustre* L. Marsh Arrow Grass (EA3, FN)

Lemnaceae

- Lemna minor* L. Lesser Duckweed (EA2, SM, FN, EA3)

Liliaceae

- Alettris farinosa* L. Colicroot (WMP)
- Asparagus officinalis* L. Garden Asparagus (SM)
- Lilium michiganense* Farw. Michigan Wild Lily (SM)
- Maianthemum canadense* Desf. Wild Lily-of-the-Valley (WF, SC3, WMH)
- Polygonatum pubescens* (Willd.) Pursh Hairy Solomon's-seal (WF)
- Smilacina racemosa* (L.) Desf. False Solomon's-seal (SM, WMP)
- S. stellata* (L.) Desf. Starry False Solomon's-seal (SC2, WF, SM, FN)
- **Smilax herbacea* L. Carrion-flower (WMH)
- S. lasioneura* Hook. Carrion-flower (WF, SM)
- Tofieldia glutinosa* (Michx.) Pers. False Asphodel (EA3, FN)
- Trillium cernuum* L. Nodding Trillium (WMH)
- T. flexipes* Raf. Drooping Trillium (SC1, WMH)
- Zigadenus glaucus* (Nutt.) Nutt. White Camas (FN)

Orchidaceae

- Corallorhiza odontorhiza* (Willd.) Nutt. Fall Coral-root (WMH)
- Cypripedium acaule* Ait. Stemless Lady's Slipper (WF)
- **C. calceolus* var. *parviflorum* (Salisb.) Fern. Small Yellow Lady's Slipper (FN)

- C. calceolus* var. *pubescens* (Willd.) Correll Large Yellow Lady's Slipper (WF, SC1)
 **C. candidum* Willd. White Lady's Slipper (FN, WF)
C. reginae Walt. Showy Lady's Slipper (SC1, WF, SM)
 **Habenaria ciliaris* (L.) R. Br. Orange Fringed Orchid (WMP)
H. dilatata (Pursh) Hook. Tall White Bog Orchid (SM)
H. psychodes (L.) Spreng. Purple Fringed Orchid (SM)
Liparis loeselii (L.) Rich. Green Twayblade (SM)
Spiranthes cernua (L.) Rich. Nodding Ladies'-tresses (FN, EA3, WMP)

Poaceae (Gramineae)

- Agropyron repens* (L.) Beauv. Quack Grass (FN)
A. trachycaulum (Link) Malte Wheatgrass (SM, FN)
Agrostis gigantea Roth Redtop (SM, WF, FN)
A. hyemalis (Walt.) BSP Ticklegrass (SM)
A. perennans (Walt.) Tuckerm. Autumn Bent (WF)
Andropogon gerardii Vitm. Big Bluestem (FN, WMP, SM)
Bromus ciliatus L. Fringed Brome (FN, SM, EA3, WF)
Calamagrostis canadensis (Michx.) Beauv. Blue-joint (SM, EA3, FN)
 **C. stricta* (Timm) Koeler Narrow Reed Grass (FN, EA1)
Dactylis glomerata L. Orchard Grass (SC3)
Danthonia spicata (L.) R. & S. Poverty Grass (WF)
Deschampsia cespitosa (L.) Beauv. Hair Grass (SM, FN)
Echinochloa muricata (Beauv.) Fern. Wild Millet (EA1)
Festuca ovina L. Sheep Fescue (EA1)
Glyceria canadensis (Michx.) Trin. Rattlesnake Grass (SM)
G. striata (Lam.) Hitchc. Fowl Manna Grass (SM, EA1)
Hierochloa odorata (L.) Beauv. Sweet Grass (SM)
Leersia oryzoides (L.) Sw. Cut Grass (SM)
Muhlenbergia glomerata (Willd.) Trin. Marsh Wild-timothy (FN)
M. mexicana (L.) Trin. Muhly (FN, SM)
Panicum boreale Nash Northern Panic Grass (FN, SC3, SM)
P. implicatum Britt. Panic Grass (SM)
P. lindheimeri Nash Panic Grass (SM)
Phalaris arundinacea L. Reed Canary Grass (SM, EA1)
Phleum pratense L. Timothy (SM, EA1)
Phragmites australis (Cav.) Steud. Reed (SM, FN)
Poa alsodes Gray Grove Meadow Grass (SM, EA1, FN)
P. compressa L. Canada Bluegrass (SM)
P. nemoralis L. Wood Bluegrass (WMH)
P. palustris L. Fowl Meadow Grass (SM, FN, EA3, WMH, WF)
P. pratensis L. Kentucky Bluegrass (SM, FN)
P. trivialis L. Rough Bluegrass (WF)
Sorghastrum nutans (L.) Nash Indian Grass (FN)
Spartina pectinata Link Cordgrass (FN)
Sphenopholis intermedia (Rydb.) Rydb. Slender Wedge Grass (FN, SM)

Sparganiaceae

- Sparganium americanum* Nutt. Bur-reed (EA1)

Typhaceae

- Typha latifolia* L. Cat-tail (EA2, EA3, FN, SM)

DICOTYLEDONS

Aceraceae

- Acer rubrum* L. Red Maple (WF)
A. saccharum Marsh. Sugar Maple (WHM, SM)

Anacardiaceae

- Rhus copallina* L. Shining Sumac (SM)
R. typhina L. Staghorn Sumac (SM)
Toxicodendron radicans (L.) Ktze. Poison Ivy (WF)

T. vernix (L.) Ktze. Poison Sumac (SC3, WF, SC2, SC1, SM, FN, EA3)

Apiaceae (Umbelliferae)

Angelica atropurpurea L. Purple-stemmed Angelica (SM, FN)

**Berula pusilla* (Nutt.) Fern. Cut-leaved Water Parsnip (EA1, FN)

Cicuta bulbifera L. Bulblet Water Hemlock (EA1, FN)

C. maculata L. Water Hemlock (SM, FN)

**Eryngium yuccifolium* Michx. Rattlesnake Master (WMP)

Osmorhiza claytoni (Michx.) Clarke Sweet Cicely (WMH)

Oxypolis rigidior (L.) Raf. Cowbane (FN, EA3, WF, SM)

Sanicula marilandica L. Black Snakeroot (WMH)

Zizia aurea (L.) Koch Golden Alexanders (FN)

Aquifoliaceae

Ilex verticillata (L.) Gray Winterberry (SC3)

Nemopanthus mucronatus (L.) Trel. Mountain Holly (WF, SC2)

Asclepiadaceae

Asclepias incarnata L. Swamp Milkweed (SM, FN)

A. syriaca L. Common Milkweed (SM, FN)

Asteraceae (Compositae)

Achillea millefolium L. Common Yarrow (SM, WF)

Ambrosia artemisiifolia L. Lesser Ragweed (SM)

Aster ericoides L. Aster (WMH)

A. junciformis Rydb. Bog Aster (FN, WF, EA3)

A. lucidulus (Gray) Wieg. Glossy-leaved Aster (EA1, SM, FN, WF)

A. macrophyllus L. Large-leaved Aster (WMH)

A. novae-angliae L. New England Aster (FN)

A. pilosus Willd. Heath Aster (SM)

A. puniceus L. Purple-stemmed Aster (FN, SM, EA1, WF)

A. sagittifolius Willd. Arrow-leaved Aster (WMH)

A. simplex Willd. Aster (FN, WF)

A. umbellatus Mill. Flat-topped Aster (FN, SM)

Bidens cernua L. Nodding Bur Marigold (EA1, SM)

B. coronata (L.) Britt. Tickseed Sunflower (EA1, FN)

Cacalia plantaginea (Raf.) Skinner Tuberous Indian Plantain (FN)

Cirsium muticum Michx. Swamp Thistle (SM, FN, WF, WMP, EA3)

C. vulgare (Savi) Tenore Bull Thistle (SM)

Coreopsis tripteris L. Tall Tickseed (FN, WMP, SM)

Erigeron pulchellus Michx. Robin's-plantain (SM)

Eupatorium maculatum L. Joe-pye Weed (SM, FN, WF, EA3)

E. perfoliatum L. Boneset (SM, FN, EA3)

Helianthus giganteus L. Giant Sunflower (FN, SM, WMP)

Krigia biflora (Walt.) Blake Dwarf Dandelion (SM, WF, SC3, FN)

Lactuca biennis (Moench) Fern. Lettuce (SM)

L. canadensis L. Lettuce (SM, FN, WMH)

Liatris spicata (L.) Willd. Blazing Star (FN)

Prenanthes altissima L. Tall White Lettuce (SM)

P. racemosa Michx. Glaucous White Lettuce (SM)

Rudbeckia hirta L. Black-eyed Susan (SM, FN, EA3, WF)

R. laciniata L. Coneflower (SM, EA1)

Senecio aureus L. Golden Ragwort (SC1, WF, WMH, SM, FN, EA3)

**Silphium integrifolium* Michx. Entire-leaved Rosinweed (FN)

Solidago caesia L. Blue-stemmed Goldenrod (WMH, WF)

S. canadensis L. Canada Goldenrod (SM, FN, EA3)

S. gigantea Ait. Great Goldenrod (SM, FN)

S. graminifolia (L.) Salisb. Flat-topped Goldenrod (SM)

S. ohioensis Riddell Ohio Goldenrod (FN, EA3)

S. patula Muhl. Swamp Goldenrod (SM, FN, WF, EA3, EA2)

S. riddellii Frank Prairie Goldenrod (FN)

S. rugosa Mill. Rough-leaved Goldenrod (SM, FN)

- S. uliginosa* Nutt. Goldenrod (FN, EA3)
Taraxacum officinale Weber Common Dandelion (SM, WF, SC3)
Vernonia altissima Nutt. Tall Purple Ironweed (SM, WMP)
V. missurica Raf. Purple Ironweed (WMP)

Balsaminaceae

- Impatiens biflora* Walt. Touch-me-not (WMH, SM, WF, FN, EA2, EA3)

Berberidaceae

- Berberis thunbergii* DC. Japanese Barberry (WF)
Podophyllum peltatum L. May Apple (WMH)

Betulaceae

- Alnus rugosa* (Du Roi) Spreng. Speckled Alder (WMH)
Betula alleghaniensis Britt. Yellow Birch (WMH)
B. pumila L. Dwarf Birch (SC2, FN, EA3, WF, SM)
Carpinus caroliniana Walt. Blue Beech (WF)
Corylus americana Walt. American Hazelnut (SM)

Brassicaceae (Cruciferae)

- Barbarea vulgaris* R. Br. Yellow Rocket (SC3)
Cardamine bulbosa (Schreb.) BSP. Spring Cress (SM, WF)
C. pratensis var. *palustris* Wimm. & Grab. Cuckoo Flower (SC1, FN, SM)
Nasturtium officinale R. Br. Watercress (EA1, FN)

Campanulaceae

- Campanula aparinoides* Pursh Blue Marsh Bellflower (FN, EA3)

Caprifoliaceae

- Lonicera canadensis* Marsh. Fly Honeysuckle (WF)
L. dioica L. Wild Honeysuckle (WF, WMH)
L. tatarica L. Tartarian Honeysuckle (WMH)
Sambucus canadensis L. Common Elder (SM, FN, WF)
Viburnum lentago L. Nannyberry (WF)

Caryophyllaceae

- Cerastium nutans* Raf. Nodding Chickweed (SM)
C. vulgatum L. Common Mouse-ear Chickweed (WMH)
Stellaria longifolia Muhl. Long-leaved Stitchwort (FN, SM)

Convolvulaceae

- Convolvulus americanus* Sims Hedge Bindweed (SC1, SM, FN)
Cuscuta gronovii Willd. Common Dodder (SC1, SM)

Cornaceae

- Cornus alternifolia* L.f. Alternate-leaved Dogwood (WF)
C. florida L. Flowering Dogwood (WF, SM)
C. racemosa Lam. Gray Dogwood (SC1, SM, FN, WF)
C. stolonifera Michx. Red-osier Dogwood (SC2, WF, SM, FN)
Nyssa sylvatica Marsh. Black Gum (WMH)

Crassulaceae

- Penthorum sedoides* L. Ditch Stonecrop (SM)

Droseraceae

- Drosera rotundifolia* L. Round-leaved Sundew (EA3, FN)

Ericaceae

- Gaultheria procumbens* L. Common Wintergreen (WMH)
Monotropa uniflora L. Indian Pipe (WMH)
Pyrola rotundifolia L. Round-leaved Wintergreen (WMH)
Vaccinium corymbosum L. Northern Highbush Blueberry (WF, SC3, SM)
V. lamarkii Camp Lamarck's Sugar Blueberry (WF)
V. myrtilloides Michx. Canadian Blueberry (WF, WMH)

Euphorbiaceae

- Euphorbia corollata* L. Flowering Spurge (SM)

Fabaceae (Leguminosae)

- Amphicarpa bracteata* (L.) Fern. Hog Peanut (WMH, FN)
Apios americana Medic. Potato Bean (SM, FN, EA3)

- Lathyrus palustris* L. Marsh Pea (FN, SM, EA3, SC2, WF, EA2)
Desmodium canadense (L.) DC. Showy Tick Trefoil (SM)
Trifolium hybridum L. Alsike Clover (SM, EA1)
Vicia americana Muhl. Vetch (SM, WMH)

Fagaceae

- Quercus bicolor* Willd. Swamp White Oak (WMH, WF)
Q. borealis var. *maxima* (Marsh.) Ashe Red Oak (WMH)
Q. palustris Muench. Pin Oak (WF, WMH)
Q. velutina Lam. Black Oak (WMH)

Gentianaceae

- Gentiana andrewsii* Greisb. Closed Gentian (FN, WMP, SM)
G. procera Holm Fringed Gentian (FN, EA3)

Geraniaceae

- Geranium maculatum* L. Wild Cranesbill (SM, SC1, FN, WMH)

Hypericaceae

- Hypericum mutilum* L. Small-flowered St. John's-wort (EA1, EA3, SM)
H. punctatum Lam. Spotted St. John's-wort (SM, WMP)

Lamiaceae (Labiatae)

- Lycopus americanus* Muhl. Water Horehound (SM, FN, EA2, WF, EA3)
L. uniflorus Michx. Bugleweed (SM)
Mentha arvensis L. Field Mint (SM, FN)
Monarda fistulosa L. Wild Bergamot (FN, SM)
Prunella vulgaris L. Selfheal (WF, SC2)
Pycnanthemum virginianum (L.) Durand & Jackson Virginia Mountain Mint (SM, FN)
Scutellaria galericulata L. Marsh Skullcap (EA3, FN, WF, EA2, SM)
Stachys hyssopifolia Michx. Hedge Nettle (WMP)

Lauraceae

- Lindera benzoin* (L.) Blume Spicebush (WF)
Sassafras albidum (Nutt.) Nees Sassafras (WMH)

Lentibulariaceae

- Utricularia intermedia* Hayne Flat-leaved Bladderwort (EA3, FN)

Lobeliaceae

- Lobelia kalmii* L. Brook Lobelia (EA3, FN)
L. siphilitica L. Large Blue Lobelia (FN, WMH)

Lythraceae

- Decodon verticillatus* (L.) Ell. Swamp Loosestrife (SM)

Menispermaceae

- Menispermum canadense* L. Moonseed (WMH)

Oleaceae

- Fraxinus nigra* Marsh. Black Ash (WMH)

Onagraceae

- Circaea quadrisulcata* (Maxim.) Franch & Sav. Enchanter's-nightshade (WF)
Epilobium coloratum Biehl. Purple-leaved Willowherb (FN, WF)
E. strictum Muhl. Downy Willowherb (FN, WF)
Oenothera parviflora L. Evening Primrose (FN)
O. pilosella Raf. Sundrops (SM)

Phytolaccaceae

- Phytolacca americana* L. Common Pokeberry (WMH)

Polemoniaceae

- Phlox pilosa* L. Red Phlox (FN, SM)

Polygalaceae

- Polygala senega* L. Seneca Snakeroot (FN)

Polygonaceae

- Polygonum natans* Eat. Water Smartweed (EA1, SM)
P. punctatum Ell. Dotted Smartweed (SM)
P. sagittatum L. Arrow-leaved Tearthumb (SM, WF)
Rumex acetosella L. Red Sorrel (SC3)

- R. crispus* L. Curly Dock (SM, EA1)
R. orbiculatus Gray Great Water Dock (EA1, SM, FN)

Primulaceae

- Lysimachia quadriflorum* Sims Narrow-leaved Loosestrife (WF)
L. quadrifolia L. Whorled Loosestrife (WMH)
L. thyrsiflora L. Water Loosestrife (WF)
Trientalis borealis Raf. Star Flower (WF)

Ranunculaceae

- Anemone quinquefolia* L. Wood Anemone (SC1, WMH, SM)
A. virginiana L. Tall Anemone (WF)
Aquilegia canadensis L. American Columbine (SM)
Caltha palustris L. Marsh Marigold (SM, FN, EA3, EA2, WF)
Clematis virginiana L. Virgin's-bower (SM, SC1)
Ranunculus abortivus L. Small-flowered Crowfoot (WMH)
R. pensylvanicus L.f. Bristly Crowfoot (SM)
R. recurvatus Poir. Hooked Crowfoot (WF)
R. repens L. Creeping Buttercup (EA1)
R. septentrionalis Poir. Swamp Buttercup (SC1)
Thalictrum dasycarpum Fisch. & Lall. Tall Meadow Rue (SM, FN, WF)

Rhamnaceae

- Rhamnus alnifolia* L'Her. Alder Buckthorn (SM)
R. frangula L. Glossy Buckthorn (SM)

Rosaceae

- Agrimonia gryposepala* Wallr. Tall Agrimony (SM)
Amelanchier intermedia Spach Juneberry (WF)
Aronia melanocarpa (Michx.) Ell. Black Chokeberry (SC1, SM, WMP)
A. prunifolia (Marsh.) Rehder Purple Chokeberry (SC1, WMH, WF)
Crataegus pruinosa (Wendl.) Koch Hawthorn (WMH)
Fragaria virginiana Duchesne Wild Strawberry (SM, FN, WF, WMP, SC1, WMH)
Geum aleppicum Jacq. Yellow Avens (EA1, SM)
G. canadense Jacq. White Avens (SM, SC2, WF)
Potentilla fruticosa L. Shrubby Cinquefoil (FN, SC2, EA3)
P. norvegica L. Cinquefoil (SM)
P. simplex Michx. Cinquefoil (SM, FN)
Prunus pumila L. Sand Cherry (WMP, SM)
P. serotina Ehr. Wild Black Cherry (WF, SM, FN, WMP)
P. virginiana L. Choke Cherry (SM)
Pyrus malus L. Common Apple (SM)
Rosa multiflora Thunb. Multiflora Rose (SC3—probably introduced)
R. palustris Marsh. Marsh Rose (SM, FN, WF)
Rubus allegheniensis Porter Allegheny Blackberry (SM)
R. hispidus L. Swamp Dewberry (SM, FN, WMP)
R. pubescens Raf. Dwarf Red Raspberry (WF, SC1)
R. setosus Bigel. Dewberry (SM)
R. strigosus Michx. Wild Red Raspberry (SM)
Spiraea alba Du Roi Meadowsweet (SM, FN)
S. tomentosa L. Hardhack (SM, FN)

Rubiaceae

- Galium aparine* L. Cleavers (WMH, WF)
G. asprellum Michx. Rough Bedstraw (WMH)
G. boreale L. Northern Bedstraw (FN, SM, EA3)
G. palustre L. Marsh Bedstraw (SM)
G. triflorum Michx. Sweet-scented Bedstraw (WMH, WF, SM)
Mitchella repens L. Partridge-berry (WF)

Salicaceae

- Populus deltoides* Marsh. Cottonwood (WMH)
P. grandidentata Michx. Large-toothed Aspen (SM, WMH)
P. tremuloides Michx. Trembling Aspen (SM, WMH, SC3)

- Salix bebbiana* Sarg. Beaked Willow (SM, SC2)
S. candida Fluegge Sage Willow (FN, SM)
S. humilis Marsh. Prairie Willow (WMP)
S. lucida Muhl. Shining Willow (SM, SC2)
S. nigra Marsh. Black Willow (SM)
S. serissima (Bailey) Fern. Autumn Willow (SM, FN)
- Santalaceae**
Comandra umbellata (L.) Nutt. Bastard Toadflax (FN)
- Sarraceniaceae**
Sarracenia purpurea L. Pitcher Plant (WF)
- Saxifragaceae**
Heuchera richardsonii R. Br. Alum-root (WMH)
Parnassia glauca Raf. Grass-of-Parnassus (EA3, FN)
Ribes hirtellum Michx. Low Wild Gooseberry (SC2, SM, FN, WF)
Saxifraga pensylvanica L. Swamp Saxifrage (SM)
- Scrophulariaceae**
Agalinis purpurea (L.) Pennell Purple Gerardia (EA3, FN)
Aureolaria flava (L.) Farw. Smooth False Foxglove (WMP)
A. pedicularis (L.) Raf. Clammy False Foxglove (WMP)
Castilleja coccinea (L.) Spreng. Indian Paintbrush (Yellow Form) (FN)
Chelone glabra L. Turtlehead (SC2, EA1)
Mimulus ringens L. Square-stemmed Monkey Flower (SC1, WMH)
Pedicularis canadensis L. Early Wood Betony (WMP)
P. lanceolata Michx. Swamp Wood Betony (FN, EA3)
Veronica catenata Penn. Water Speedwell (EA1)
Veronicastrum virginicum (L.) Farw. Culver's-root (FN, SM)
- Solanaceae**
Solanum dulcamara L. Bitter Nightshade (SC1, SM, WF, EA1)
- Tiliaceae**
Tilia americana L. Basswood (SM)
- Ulmaceae**
Ulmus rubra Muhl. Red Elm (WMH, WF)
- Valerianaceae**
Valeriana uliginosa (T. & G.) Rybd. Swamp Valerian (FN, WF)
- Verbenaceae**
Verbena hastata L. Blue Vervain (FN, SM)
- Violaceae**
Viola cucullata Ait. Marsh Violet (EA1, EA3, FN, WF)
V. eriocarpa Schw. Stemmed Yellow Violet (SC1)
V. pallens (Banks) Brainerd Smooth White Violet (WF, SC1)
V. sagittata Ait. Arrow-leaved Violet (SC3, SM)
V. sororia Willd. Hairy Blue Violet (WMH)
- Vitaceae**
Parthenocissus quinquefolia (L.) Planch. Virginia Creeper (WF, WMH)
Vitis riparia Michx. River-bank Grape (WF)

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THE DISTRIBUTION AND AUTECOLOGY OF
PALE AGOSERIS, AGOSERIS GLAUCA,
IN MICHIGAN¹

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In 1973, one to two tons of the toxic fire retardant, polybrominated biphenyl (PBB), were accidentally mixed into an animal feed supplement and fed to livestock in Michigan. Approximately 250 dairy and 500 cattle farms were subsequently quarantined, and tens of thousands of swine and cattle and more than one million chickens were destroyed. Before the nature of the contamination was recognized, many of the contaminated animals had been slaughtered, marketed, and eaten, thus exposing much of Michigan's human population to PBB.

In 1979 the Michigan Dept. of Natural Resources began burying contaminated livestock in large clay-lined pits near Mio, in northwestern Oscoda County. A large population of *Agoseris glauca* (Pursh) Raf., a Michigan threatened plant species which occurred at the burial site, was destroyed during excavation and burial activities. At that time the size of the pale agoseris population in Michigan was not known and thus the extent of damage to the species was uncertain. The author was contracted by the Michigan Dept. of Natural Resources during the summer of 1979 to conduct a study of the distribution and ecological requirements of pale agoseris in Michigan and to assess the extent to which the species had been adversely affected by the burial activities.

Agoseris glauca is a member of the composite family (Asteraceae, subfamily Cichorioideae). These perennial plants have yellow, solitary flower heads which extend 1–5 cm above the base of the plant (Fig. 1). The involucre bracts are 1–3 cm long, imbricate, sharply pointed, and usually purple-spotted. The seeds, possessing a well-developed pappus, are wind dispersed. The leaves, confined to a basal rosette, are glabrous, linear, or oblanceolate with entire to slightly pinnatifid margins. The plants arise from a deep taproot and, like all members of the subfamily, contain milky sap. The species consists of five varieties (Jones, 1954). All of the Michigan specimens appear to be *A. glauca* var. *glauca*. The total continuous range of the species extends from British Columbia to California and Arizona eastward to Manitoba and western Minnesota (Hitchcock et al., 1971). A disjunct population occurs in the jack pine plains of Michigan at the contiguous corners of Otsego, Montmorency, Oscoda, and Crawford Counties (Fig. 2).

¹This article represents a summary of a report prepared for the Michigan DNR (Mustard, 1979).

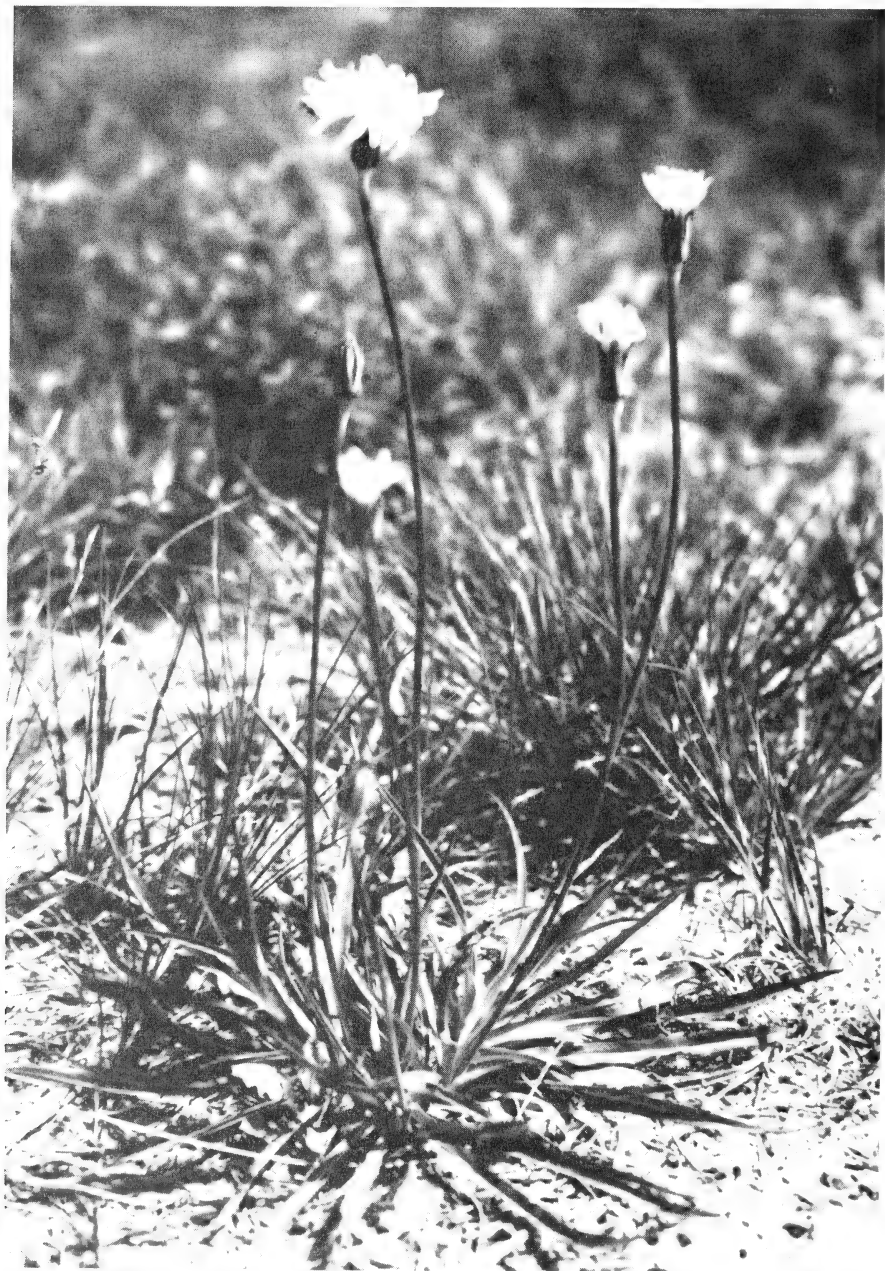


Fig. 1. Pale agoseris, *Agoseris glauca*. Photographed 6 June 1979.

All the Michigan *Agoseris* localities are situated on a large glacial outwash formation located on or within a few miles of the watershed divide between the Thunder Bay and AuSable drainage basins (Michigan Dept. of Agriculture, undated). The topography is level to gently rolling. The mean height above sea level is approximately 1200 feet (range 1000 to 1280 feet). Most of the collection localities occur on well drained sands of the Grayling Series (Veatch et al., 1927, 1930, 1931). A few localities occur on Rubicon sand. The climate of the four-county area included in this study is continental in character. Unlike counties bordering on the Great Lakes with an ameliorated climate, conditions in this region are more extreme. Temperatures ranging from 112°F to -47°F have been recorded at the Mio weather station (Michigan Dept. of Agriculture, 1971). The mean annual temperature is approximately 43°, and the growing season averages 102 days. Mean annual precipitation is 30 inches, but because of relatively high evapotranspiration rates drought conditions frequently occur.

Information concerning collection localities in Michigan was obtained from DNR data cards prepared by Mark Böhlke and Jonathan Wendel and from inspection of herbarium specimens at MSC and MICH. The 11 previously known localities were visited and the presence of *Agoseris* confirmed at all but three. In addition, a thorough search was made for the species in outlying portions of the four-county area.

Twenty 10-m diameter circular plots (relevés) were established in various *Agoseris* communities to estimate the relative abundance of the species and semi-quantitatively describe the vegetational associates. All plant species circumscribed within each plot were recorded. A cover-density rating was assigned to each species following methods adapted from Braun-Blanquet (1932) and Taylor (pers. comm.). The scale used was as follows:

Cover Scale	Density Scale
+ cover <1%	1 one only
1 cover 1-5%	2 2-10 individuals
2 cover 5-15%	3 11-100 individuals
3 cover 25-50%	4 > 100 individuals
4 cover 50-75%	
5 cover >75%	

The two scales were combined to establish a cover-density rating such as +/1, where the first symbol refers to the coverage by a species and the second to density (Table 1).

Notes recorded at each relevé locality included topography, conditions of disturbance, population size, and population vigor. Soil samples were taken in typical relevé plots and in outlying areas where *Agoseris* was expected but not found. The soil samples were analyzed by the Michigan State University Soil Testing Laboratory for pH, nutrients, and particle size. Voucher specimens of pale agoseris and its community associates are deposited in MSC.

Agoseris was typically found in xeric, grassy clearings in the jack pine association. Low shrubs such as blueberry (*Vaccinium angustifolium*), sweet fern (*Comptonia peregrina*), and sand cherry (*Prunus pumila*) were frequent community components. Devil's paint brush (*Hieracium aurantiacum*) and terricolous lichens were often abundant. Although many areas showed evidence of logging and fire, these communities appeared relatively mature with no detectable disturbance within the past 15 years.

Pale agoseris was often found in topographic depressions ("frost pockets") and was generally more abundant at the bottom of the depression. (The role of microclimate in influencing the distribution of the species warrants further study.) In all cases *Agoseris* was found growing in well-drained medium to fine sands of the Grayling or Rubicon series. Soil pH ranged from 5.1 to 6.7 in the sample plots.

The distribution of pale agoseris mapped in Figure 2 includes two large distributional centers: one in the Bear Lake area of southeastern Otsego Co. and the other near the burial site in north-central Oscoda Co. The population centered about the PBB burial pit site is by far the best-developed stand in Michigan. The plants are particularly abundant adjacent to the site. Isolated stands can be found north and northwest of the site. The Bear Lake population of southeastern Otsego County occupies approximately 26 square kilometers. The species is locally abundant in grassy clearings throughout the area. It should be noted that another threatened plant, *Festuca scabrella* (Poaceae), is frequently encountered in grassland habitats throughout the Bear Lake area. A third well-developed *Agoseris* population occurs in northeastern Crawford County. This population attains its best development in and near the Lovells Management area for Kirtland's Warbler.

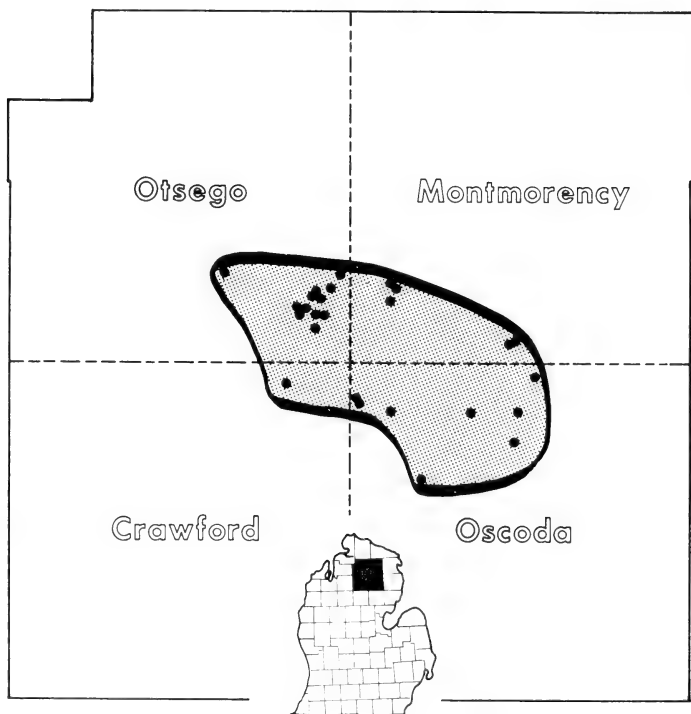


Fig. 2. Distribution of *Agoseris glauca* in Michigan. Dots show localities supported by voucher specimens.

Frequency values and cover-density estimates for species associated with *Agoseris* are presented in Table 1. Because the relevé plots were chosen to include *Agoseris*, it possesses a frequency value of 100%. *Hieracium aurantiacum* was very frequent, being found in 16 of the 20 relevés. *Vaccinium angustifolium* was present in 14 of the 20 plots. *Comptonia peregrina* was found in over half of the relevés. The cover-density estimates illustrate the importance of various species. *Agoseris* generally had low density (few individuals per unit area) and low dominance (percent cover). Grasses were generally the dominant plants in terms of cover and abundance. Devil's paint-brush and blueberry were usually represented by numerous individuals with moderate to large coverage. Small jack pines were encountered in a few relevés. *Agoseris* was rarely found under mature pines. Rather, it exhibited a marked preference for open, shrub-grassland habitats.

Burial of PBB-contaminated livestock extirpated plants growing on the burial site, although the species is still well represented in adjacent clearings. At this time it is not known if the general population is increasing or decreasing. The species was not found at three of the 11 previously known localities. However, two of these localities were too general ("near Comins" and "Pigeon River State Forest") to be accurately located. The third was in an area designated Kirtland Warbler habitat and was inaccessible to the author during the time the survey was conducted.

In light of the limited distribution of pale agoseris in Michigan, measures should be taken to minimize impacts in the future. Possible means of mitigating future impacts to *Agoseris glauca* have been suggested to the Michigan DNR (Mustard, 1979), including the following: (1) Notation of its presence on State Forest Ownership Cards. Because these cards are examined prior to management action on state forest lands, notations regarding *Agoseris glauca* (or other protected species) would greatly reduce future adverse effects. (2) Maintenance of critical grassland habitats by clear cutting and/or controlled burning. This would be especially feasible in areas managed as Kirtland Warbler habitat. Small, open grassland associations could be maintained in Warbler habitats, thereby creating a favorable habitat for pale agoseris.

Further studies, particularly demographic, are necessary to provide a complete understanding of reproductive and life history aspects of the species. It is my hope that Michigan universities and the Michigan Dept. of Natural Resources will encourage and support research on this and other threatened and endangered plants in Michigan.

SUMMARY

The distribution and ecological requirements of *Agoseris glauca* (a threatened plant species in Michigan) were determined. *Agoseris* was found to be restricted to dry, sandy soils at the contiguous corners of Crawford, Montmorency, Oscoda, and Otsego Counties in north-central Michigan. The preferred habitat was found to be open shrub-grassland communities in the jack pine association. Recommendations are made specifying measures to be taken to minimize future adverse effects to the species.

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NOTICE

As an economy measure, the 3-year cumulative index has been discontinued. It is planned, however, that an index will be published, very likely at the end of volume 25.

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On the cover: *A stand of Nelumbo lutea, American Lotus,*
with *Myriophyllum heterophyllum* (and *Heteranthera*
dubia) at Big Rice Bay, Long Point, Norfolk Co.,
Ontario; photo by P. M. Catling, Aug. 3, 1980

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